North American River Otter *(Lontra canadensis)*: A Technical Conservation Assessment

**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

September 2, 2006

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Boyle, S. (2006, September 2). North American River Otter (*Lontra canadensis*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/northamericanriverotter.pdf [date of access].

ACKNOWLEDGMENTS

AUTHOR'S BIOGRAPHY

Steve Boyle is Senior Biologist and owner of BIO-Logic Environmental in Montrose, Colorado. He holds an MS degree in Wildlife Biology (Colorado State University, 1981) and has 27 years of experience in biological assessments, natural resource planning, and wildlife management and research in the western U.S. and overseas. He authored the Forest Service Region 2 Beaver Species Conservation Assessment, and has led a number of regional conservation planning efforts including a Sagebrush Steppe Ecosystem Conservation Assessment and Management Plan for the Colorado Division of Wildlife, and Statewide Programmatic Biological Evaluations for four grouse species in Colorado for the USDI Bureau of Land Management.

As former Senior Wildlife Biologist for AGEISS Environmental, Inc., Mr. Boyle was Principal Investigator for research projects on pronghorn, feral horses, bats, and songbird communities at U.S. Army Dugway Proving Ground, Utah. He has other research experience investigating spotted owls, kit fox, mule deer, elk, bighorn sheep, wild turkey, river otter, and desert tortoises. He was an invited reviewer of the Colorado Gap Analysis Project and more recently the Southwest Regional GAP Analysis Project, critically reviewing theoretical models linking vertebrate species distributions to habitat characteristics. He performed extensive fieldwork for and co-authored the Colorado Breeding Bird Atlas. Prior to consulting work, Mr. Boyle was District Wildlife Manager for the Colorado Division of Wildlife, Research Technician for the U.S. Fish and Wildlife Service, and Research Associate of the Department of Fishery and Wildlife Biology, Colorado State University.

COVER PHOTO CREDIT

North American River Otter (*Lontra canadensis*). Photograph by Eric Peterson. Used with permission.

Summary of Key Components for Conservation of The North American River Otter

Status

The North American river otter (*Lontra canadensis*) occurs in streams, lakes and reservoirs, wetlands, and marine coasts. The species occurs broadly across much of North America and is considered reasonably secure overall. Severe declines in the 1800's from unregulated fur harvest and habitat destruction extirpated or severely reduced populations in many parts of the United States, including much of the USDA Forest Service (USFS), Rocky Mountain Region (Region 2) area. River otters were extirpated from Colorado and Nebraska, nearly extirpated from South Dakota and Kansas, and severely reduced in Wyoming. Regulation of trapping, improved water quality, and intensive management, including translocations, have re-established the species to much of its former range in North America. Reintroductions in all Region 2 states except Wyoming have re-established river otters to some of its former range, and otter populations appear to be expanding into additional remaining suitable habitat.

The river otter is listed as a Sensitive Species by the USFS throughout Region 2, as state threatened by the states of Colorado, Nebraska, and South Dakota, and protected under state laws in all states within Region 2.

Primary Threats

Principal threats are habitat destruction and degradation, and human-caused mortality. Habitat destruction and degradation include water development resulting in stream flow and channel morphology alteration, water pollution, loss of riparian vegetation, and human settlement and recreational use along rivers and lakes. Water development is a widespread and increasing threat in most watersheds across Region 2 and may affect river otter populations at local and regional scales. Increasing human settlement, with the resulting increases in water development and recreational use, is the most immediate threat to river otter population viability in many watersheds throughout Region 2. Water pollution is a localized threat in some mountain drainages streams in Colorado and Wyoming, and a more pervasive threat in lower stream reaches. Water pollution that reduces or eliminates otter prey populations (fish and invertebrates) is a threat at local scales to some otter populations or potential habitats. Human recreational use of streams, lakes, and reservoirs is a localized and increasing threat in some watersheds, particularly in Colorado and parts of Wyoming. Human settlement along rivers, lakes, and reservoirs also is an increasing threat in many watersheds, particularly in Colorado. Development is increasingly likely to affect many river otter populations and potential habitats at watershed and regional scales. Agricultural use of riparian areas is a threat in the lower reaches of most watersheds in Region 2.

Human-caused mortality is a localized but increasing threat in some watersheds throughout Region 2. Accidental take in beaver (*Castor canadensis*) traps occurs primarily in states other than Colorado, where regulations restrict beaver trapping; however, accidental take is not thought to be a serious threat to most otter populations. Roadkill occurs where highways closely encroach on rivers; the degree of the threat is unknown, but it may be substantial for some otter populations, particularly in Colorado. Predation by dogs is a highly localized but increasing threat where residential use impinges on river otter habitats, particularly in Colorado. To a lesser extent, illegal trapping and shooting also occur. These are probably highly localized and not imminent threats.

Primary Conservation Elements, Management Implications and Considerations

Key conservation elements for the river otter include:

- ❖ protect instream flow, seasonal flow regimes, and water quality
- ❖ protect riparian vegetation and physical structure of banks and floodplains
- ❖ maintain and enhance aquatic prey populations
- ❖ protect habitat areas of sufficient size and maximize habitat connectivity
- ❖ control human-caused mortality.

Key management steps to achieve these conservation elements include:

- ❖ continue state regulatory controls on commercial harvest and legal take, and periodically review for adequacy
- ❖ continue statewide population monitoring in Colorado and Nebraska, and institute habitat monitoring where habitat degradation is a concern
- ❖ manage public land uses to avoid or mitigate degradation of river otter habitat, particularly with respect to timber harvest, livestock grazing, fisheries and water resources management, and roads in riparian areas
- ❖ form multi-agency partnerships to evaluate river otter habitat at landscape scales across jurisdictional boundaries, and recommend and implement planning to protect large habitat reaches and connectivity between habitat areas.

Key research needs include developing reliable and cost-effective population monitoring techniques, improving population models, and understanding the effects of habitat degradation on river otter reproduction and population viability.

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INTRODUCTION

This conservation assessment is one of many being produced to support the Species Conservation Project for the USDA Forest Service (USFS), Rocky Mountain Region (Region 2) (**Figure 1**). The North American river otter (*Lontra canadensis*; hereafter, river otter) is the focus of an assessment because USFS Region 2 classifies it as a sensitive species. Within the National Forest System (NFS), a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance or significant current or predicted downward trends in habitat capability that would reduce its distribution (FSM 2670.5 (19)). A sensitive species may require special management, so knowledge of its biology and ecology is critical.

This assessment addresses the biology, ecology, status, conservation, and management of the river otter throughout its range in Region 2. The broad nature of the assessment leads to some constraints on the specificity of information for particular locales. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal of Assessment

Species conservation assessments produced for the Species Conservation Project are designed to provide land managers, biologists, and the public with a thorough discussion of the biology, ecology, status, conservation, and management of certain species. This assessment is based on current scientific knowledge, discussion of implications of that knowledge, and outlines of information needs. While it does not prescribe management, it does provide the ecological and conservation biology background upon which managers must base their decisions. The assessment focuses on the conservation needs of the species and consequences of changes in the environment that result from management (i.e., management implications). Furthermore, it cites management
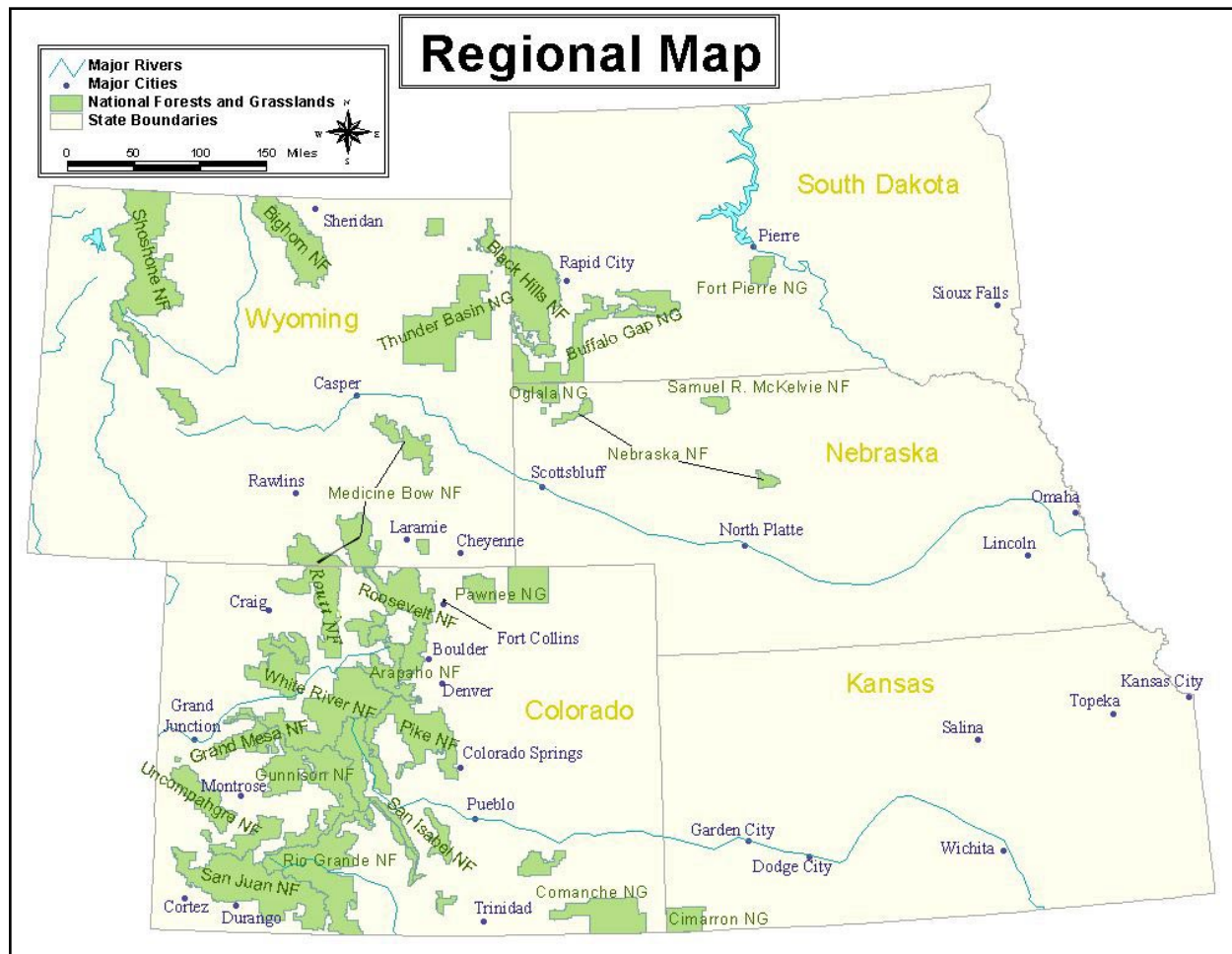

Figure 1. National forests and grasslands within USDA Forest Service Region 2.

recommendations proposed or undertaken elsewhere, and when recommendations have been implemented, the assessment examines their effectiveness.

Scope of Assessment

This conservation assessment examines the biology, ecology, status, conservation, and management of the river otter with specific reference to the geographic and ecological characteristics of Region 2. Although much of the literature on river otters originates from field investigations outside the region, this document places that literature in the ecological and social contexts of the central and southern Rocky Mountains.

In producing the assessment, I reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on river otters are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. While non-refereed publications or reports were regarded with greater skepticism, I chose to use some non-refereed literature when refereed information was unavailable. Unpublished data (e.g., Natural Heritage Program records and state agency monitoring and translocation reports) were important in estimating the geographic distribution of this species. These data required special attention because of the diversity of persons and methods used in its collection.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and observations limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, strong inference suggests that experiments will produce clean results (Hilborn and Mangel 1997), as may be observed in certain physical sciences. The geologist, T. C. Chamberlain (1897) suggested an alternative approach to science where multiple competing hypotheses are confronted with observation and data. Sorting among alternatives may be accomplished using a variety of scientific tools (e.g., experiments, modeling, and

logical inference). As in geology, there is difficulty in conducting critical experiments in ecology, so we must rely on observation, inference, good thinking, and models to guide our understanding of the world (Hilborn and Mangel 1997). In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate.

The greatest uncertainties encountered in this assessment involved river otter abundance estimates, otter fertility and survival, and the effects of human-caused habitat changes on river otter populations. River otter presence is relatively easy to detect by sign surveys, but no field techniques exist to reliably census the species. As a result, knowledge of river otter abundance is essentially nil for the entire region, other than what can be inferred from assumptions about density based on home range size estimates. The assessment deals with that uncertainty by stating state agency population estimates where they exist, identifying the uncertain assumptions on which they are based, and attempting no further analysis of abundance.

The population matrix analyses in this assessment are based on incomplete knowledge of fertility and survival rates. The degree to which environmental conditions are influenced negatively or positively by management may affect life history characteristics. All published reports of age-specific fertility are from studies outside of Region 2. Much variation exists in reported age at first breeding and the extent to which adult females breed every year. I assumed that Region 2 river otter reproductive rates are similar to those reported for the nearest geographic regions and most climatically similar regions (i.e., Idaho and north-central United States). Age-specific survival rates have only been reported for a few populations, all far from Region 2. Furthermore, the studied populations were all subject to commercial trapping (i.e., carcasses of trapped animals provided the study specimens). I averaged survival rates from two reported studies for analysis in this assessment.

Finally, no direct measurement data exist on the effects of human-caused habitat alteration on river otters. Consequently, the potential responses of otter populations to habitat degradation and restoration are highly speculative. I used information on river otter habitat requirements and inferences from monitoring reports and personal knowledge of habitat conditions in some areas of Colorado to develop conservation considerations.

Publication of Assessment of the World Wide Web

Species conservation assessments are being published on the Region 2 World Wide Web site (http://www.fs.fed.us./r2/projects/scp/assessments/index.shtml) to make them available to agency biologists and managers, and the public more rapidly than publication as a book or report, and to facilitate updates and revision, which will be accomplished based on procedures established by Region 2.

Peer Review

In keeping with the standards of scientific publication, assessments developed for the Species Conservation Project have been externally peer reviewed prior to their release on the Web. This assessment was reviewed through a process administered by the Society for Conservation Biology, which chose two recognized experts (on this or related taxa) to provide critical input on the manuscript.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

As of August 2006, USFS Region 2 lists the river otter as a sensitive species throughout the region (http://www.fs.fed.us/r2/projects/scp/sensitivespecies/index.shtml). In addition, it is a Management Indicator Species on the San Juan National Forest.

Regulatory and management authority for river otters within Region 2 rests primarily with the states. Management status of this species in Region 2 states ranges from state threatened to protected (**Table 1**). While river otters are legally trapped in many states and in all Canadian provinces, they are protected from take by state law in all Region 2 states (Melquist et al. 2003). The North American river otter is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), not based on its own conservation status, but due to its similarity to other listed species (Melquist et al. 2003). Appendix II listing requires all exported specimens or parts to be tagged with CITES export tags from the exporting country's designated scientific authority, which certifies that the taking of the specimen does not jeopardize the species' continued existence. In the United States, the U.S. Fish and Wildlife Service (USFWS) is the designated CITES authority.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Colorado

The Colorado Division of Wildlife (CDOW) listed the river otter as state endangered in 1975 based on its apparent extirpation from the state (Colorado Division of Wildlife 2003a). State endangered status reflects a

Table 1. Legal status and Natural Heritage Program rank of the river otter in states within and adjacent to USDA Forest Service Region 2.

State	State Legal Status	CNHP State Rank
Region 2 States:		
Colorado	Threatened	Vulnerable/apparently secure (S3S4)
Kansas	Protected	Critically imperiled (S1)
Nebraska	Threatened	Imperiled (S2)
South Dakota	Threatened	Imperiled (S2)
Wyoming	Protected	Vulnerable (S3)
Adjacent States:		
Arizona	Species of special concern	Critically imperiled (S1)
Idaho	Harvested	Apparently secure (S4)
Montana	Harvested	Apparently secure (S4)
New Mexico	Extirpated	Possible extirpated (SH)
North Dakota	Not harvested	Critically imperiled (S1)
Oklahoma	Protected	Imperiled (S2)
Utah	Not harvested	Vulnerable (S3)

determination that the species is at risk of extirpation from the state, and it confers statutory protection from taking or harassment. Downlisting from state endangered to state threatened status requires the establishment of three persistent and expanding river otter populations, with each occupying at least 50 km of contiguous stream habitat. Delisting will require the establishment of three separate self-sustaining populations with each occupying 120 km of nearly contiguous river habitat. Following reintroductions of river otters that started in 1976, an initial river otter recovery plan (Goodman 1984) called for the establishment of two populations. In 2003, CDOW created a River Otter Recovery Plan (Colorado Division of Wildlife 2003b) that provides verification and measurement standards for determining population range and status based on systematic sign surveys (see Management Techniques section), and standards and protocols for additional river otter reintroductions. In about 2001, CDOW initiated systematic sign surveys on rivers where otters had been reported. In September 2003, CDOW downlisted river otters to threatened status, reflecting a determination that the species is not at immediate risk of extirpation in the state but remains vulnerable; full statutory protection from taking or harassment is maintained. CDOW continues to monitor river otter populations by sign surveys conducted once every 5 years. CDOW has also funded research to develop improved monitoring techniques, focusing on DNA "fingerprinting" of individuals. Rocky Mountain National Park in Colorado contains one of the reintroduced river otter populations in the headwaters of the Colorado River, and it has supported annual population monitoring and other habitat research on river otters since 2001 (Herreman and Ben-David 2002; unpublished research reports, Rocky Mountain National Park).

Nebraska

In Nebraska, where river otters were also extirpated and reintroduced, the Nebraska Game and Parks Commission (NGPC) has defined a goal of establishing a self-sustaining statewide population and creating a river otter recovery plan (Nebraska Game and Parks Commission 2003). Between 1986 and 1991, river otters were reintroduced at seven sites across the state (see Distribution and Abundance section). River otters were listed as state endangered in the 1980's and downlisted to state threatened in 2005, following the recommendation of a board of state species experts (S. Wilson personal communication 2006). Annual monitoring is conducted by searching for otter sign at bridge crossings. The survey provides presence-

absence data and coarse estimates of abundance and population trend by extrapolating presence data based on assumed home range size. The technique is subject to considerable bias in observability of sign between years, depending on snow conditions.

Kansas

The Kansas Department of Wildlife and Parks (KDWP) carried out a reintroduction of 19 otters in Chase County, east-central Kansas, in 1983-1984, and other otters have probably dispersed into Kansas from adjacent states (especially Missouri) in recent years (M. Peak personal communication 2003). However, KDWP has no management plan for river otters and does not conduct inventory or monitoring except for maintaining records of reported sightings and carcasses. Due to public concerns about otter predation on sport fish and damage to commercial fish farms, KDPW allows but does not encourage the expansion of existing populations. Consequently, the persistence of river otters in Kansas is not assured.

South Dakota

The South Dakota Game, Fish, and Parks Commission (SDGFP) lists the river otter as state threatened (i.e., the species is vulnerable to extirpation from the state), which provides statutory protection from taking or harassment. Kiesow (2003) analyzed the status and distribution of river otters in South Dakota, identified and prioritized possible reintroduction sites, and developed a reintroduction protocol. However, the state has no plans to recover river otters in the state, nor does it have an inventory and monitoring program.

Wyoming

In Wyoming, river otter trapping was closed in 1952, and the species has been legislatively protected from take since 1973. The Wyoming Game and Fish Department (WGFD) has not developed a management plan, nor does it inventory or monitor river otter populations (B. Oakleaf personal communication 2003). Current research through the University of Wyoming includes a study of impacts of introduced lake trout (*Salvelinus namaycush*) on otters in Yellowstone National Park (Crait et al. 2002) and population characteristics of river otters in the Green River, with reference to dispersal capabilities (Boyd and Ben-David 2002).

Other states

River otters are apparently extirpated in New Mexico, and are protected from commercial harvest in Arizona, Utah, North Dakota, and Oklahoma (Raesly 2001). Arizona, Oklahoma, and Utah have reintroduced river otters to some former ranges, but the level of success of the Arizona reintroduction is unclear (M. Bed-David personal communication 2003).

Idaho reinstated a trapping season for river otters in 2000, following closed seasons since 1972 (W. Melquist personal communication 2005). In recent years, trapping was permitted in 28 states and nearly all Canadian provinces and territories (Melquist et al. 2003). River otters are not a major part of the North American fur market, but their economic value is important because of the demand for their high quality fur (Toweill and Tabor 1982). The number of pelts sold annually has steadily increased from about 10,000 in the 1920's to over 50,000 in the late 1970's, the latter figure valued at as much as $3 million United States (Deems and Pursley 1983). State and provincial agencies manage trapping harvest generally by monitoring harvest levels and habitat because no cost-effective census techniques are available. However, economic factors strongly influence river otter harvest, so it may be an unreliable index of abundance. Because otter harvest is often incidental to beaver (*Castor canadensis*) harvest, otter harvest in the northeastern United States and eastern Canada is positively correlated with beaver harvests and with the average beaver pelt price from the previous year (Chilelli et al. 1996).

Regional management

Government agencies within Region 2 have not developed regional conservation or management planning for the river otter beyond the state plans and strategies described above. Within Region 2, this species is most securely established in western Wyoming and, to a lesser extent, western Colorado, with small populations apparently expanding in central and northern Nebraska. In western Wyoming, river otters appear to be secure and widespread in several watersheds. Suitable habitat is fairly extensive, and threats are low in most areas. However, conservation planning for river otters in Wyoming is limited and may not be adequate to ensure the maintenance of viable populations if threats such as water development projects or declines in fish prey become more pervasive. Active conservation planning in Nebraska and Colorado is contributing to the recovery of river otters in some remaining habitats of those states, but increasing threats from habitat degradation and human-caused mortality may ultimately limit the extent of recovery.

Elsewhere in Region 2, river otters are rare or extirpated. In western Kansas and South Dakota, few, small populations and the lack of conservation planning or monitoring make the continued or future existence of the species tenuous. While it is possible that river otter populations could recover in these areas by natural recolonization from other areas, the provision and maintenance of suitable habitat quality and connectivity will be essential.

Adequacy and enforcement of existing laws and regulations

Current laws and regulations in Region 2 states provide sufficient statutory protection from intentional killing and persecution of river otters. Trapping for beavers is still permitted in all Region 2 states except Colorado, and river otters are occasionally killed in beaver traps. In addition, illegal killing is known to occur. For example, a few incidents of intentional trapping of river otters for illegal sale out of state were detected in Nebraska (R. Bischof personal communication 2003). However, such incidents appear isolated, and the high public appeal of river otters lends support to compliance with regulations prohibiting trapping and take. Where populations are small and isolated, especially in parts of Colorado and the eastern tier of Region 2 states, illegal or accidental kill of even a few otters may be detrimental to some populations.

Biology and Ecology

Systematics and species description

The American Society of Mammalogists classifies the North American river otter as *Lontra canadensis*, Order Carnivora, Family Mustelidae, Subfamily Lutrinae (Larivière and Walton 1998). van Zyll de Jong (1987) recognized North and South American otters as being distinct from Eurasian otters (*Lutra*) and assigned them to the genus *Lontra*. *Lontra* includes four species, of which only one, *L. canadensis*, is found in North America north of Mexico.

A lack of specimens and high variability among individuals hamper subspecies distinctions within *Lontra canadensis* (Davis 1978). Hall and Kelson (1959) recognized 19 subspecies, but in a more recent revision, Hall (1981) consolidated these into seven. Subspecies status is now further confused in many parts of the United States including all Region 2 states by reintroductions of river otters obtained from other regions of North America (Raesly 2001).

The river otter is a somewhat stocky, yet streamlined, mustelid, weighing 5 to 14 kg with short legs, a muscular neck at least as large as the head, and an elongate body widest at the hips (Larivière and Walton 1998, Melquist et al. 2003). The tail is long and tapered, and comprises about one-third of the total length of the animal. The head is flat with a broad muzzle, the ears are small and inconspicuous, and the eyes are small and placed anteriorly. The fur is short, very dense, and lustrous. Fur color ranges from almost black to pale chestnut dorsally, and light brown to gray ventrally. Dorsal color tends to be lighter in the western and southern portions of the range (Toweill and Tabor 1982). Fur of older animals may become white-tipped, and albinos may rarely occur. Males are 5 percent (Jackson 1961) to 17 percent (Melquist and Hornocker 1983) larger than females. The average adult total lengths of three males and three females in Louisiana were 113 cm and 98 cm, respectively (Lowery 1974). Some average weights (in kg) reported for adult males and females are 7.7 and 7.3 in Alberta, Canada (Smith 1993), 9.2 and 7.9 in Idaho (Melquist and Hornocker 1983), and 9.4 and 8.4 in Alaska (Duffy et al. 1994). River otters may decrease in size along the Pacific Coast from north to south (Toweill and Tabor 1982), but no clinal pattern is evident from east to west (van Zyll de Jong 1972).

The body form of the river otter is strongly adapted for aquatic life, with short ears, a streamlined body, short powerful legs, fully webbed toes, and a long tapered tail. The body configuration provides a streamlined profile in water and powerful swimming ability, but it reduces agility on land (Tarasoff et al. 1972). Each foot has five toes, non-retractable claws, and interdigital webbing. River otters have acute senses of smell and hearing, and their paws have a delicate sense of touch and great dexterity (Park 1971). Decreased lung lobulation and a shortened trachea in river otters are apparently adaptations to increase air exchange and lung ventilation when diving (Tarasoff and Kooyman 1973a, 1973b).

Distribution and abundance

The overall historical distribution of river otters is well known from trapping records and observations of early naturalists. River otters formerly occupied most major drainages in Canada and the continental United States (**Figure 2**; Hall 1981, Melquist et al. 2003). Centers of abundance occurred in areas of rich aquatic habitats such as Pacific Northwest marine shorelines, Atlantic coastal marshes, the Great Lakes region, and New England (Melquist and Dronkert 1987, Melquist et al. 2003). River otters were also historically widespread in virtually all major waterways and marshes of the North American interior, including all Region 2 states.

Unregulated fur trapping and influences of European settlement caused a sharp decline in river
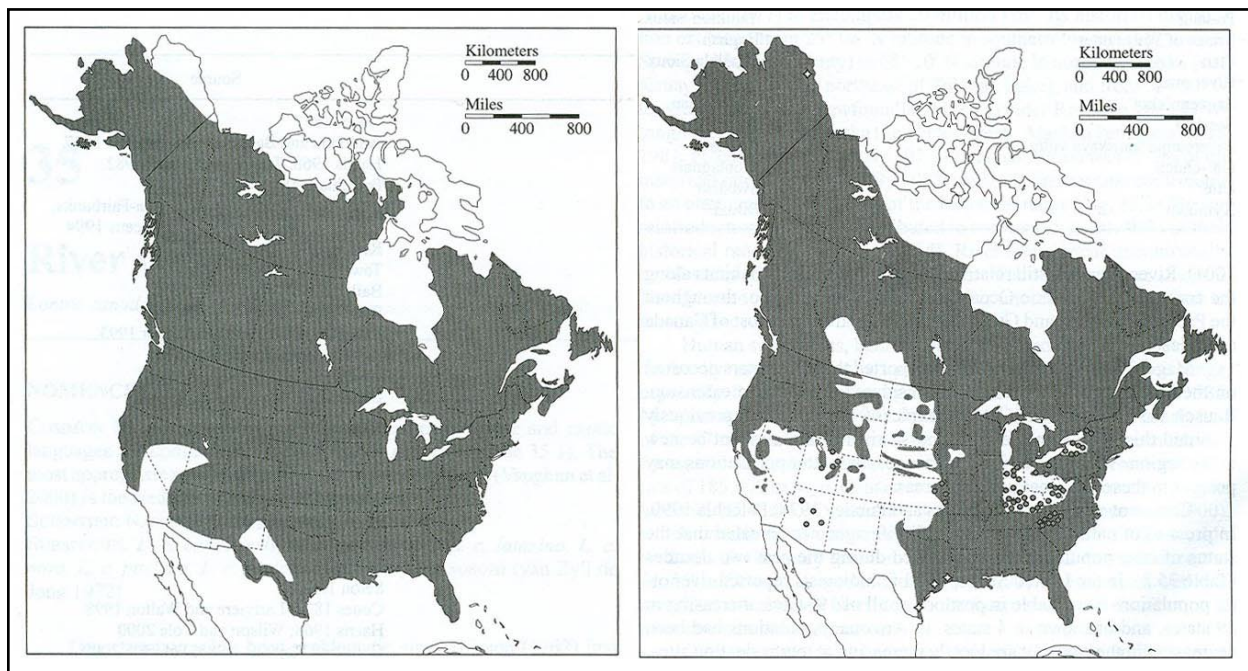

Figure 2. Historical (left) and current (right) distributions of the North American river otter. On the current distribution map, circles represent reintroduction sites. Reprinted from Melquist et al. (2003).

otter abundance and distribution. They became scarce in New England by 1700, and trappers moved farther west and south (Melquist et al. 2003). Trappers from Spanish colonies in New Mexico exerted pressure at least as far north as southern Colorado beginning in the 1700's. Fur trapping in the Region 2 area became particularly destructive to furbearers in the early 1800's, and many Region 2 river otter populations were drastically reduced or eliminated during that century (Nilsson 1980). By the mid-1900's, the North American range of the river otter was reduced to less than 75 percent of its historical extent (Melquist et al. 2003); it was extirpated from at least six states and suffered serious declines in 14 others (Raesly 2001), mostly in the continental interior. Population declines were documented in all states.

In Region 2, otters were extirpated from Colorado and Nebraska (Raesly 2001), nearly extirpated in Kansas and South Dakota, and extirpated from most of Wyoming outside of Yellowstone and Grand Teton national parks. Since 1976, improvements in furbearer management techniques and water quality, and increased concern for declining river otter populations, have spurred many recovery programs. By 1998, reintroductions in 21 states and the province of Alberta (Raesly 2001) had restored river otter distribution to nearly 90 percent of its historical range (Melquist et al. 2003). In Region 2, reintroductions have helped to restore some extirpated populations in Colorado and Nebraska, and to bolster native populations in eastern parts of South Dakota and Kansas.

Throughout North America, river otters reach their greatest densities in food-rich coastal habitats and lower stream reaches where human disturbance is low (Melquist and Dronkert 1987, Melquist et al. 2003). River otters in coastal marine habitats of the Pacific Northwest and southern Alaska reach densities two to three times that reported for interior populations (Melquist and Dronkert 1987, Bowyer et al. 2003). Inland populations reach their greatest densities in lowland or valley marshes interconnected with meandering streams and small lakes (Melquist and Hornocker 1983, Reid et al. 1994b). While river otters are relatively common in many major river systems, they become less common in heavily settled areas and in food-poor mountain streams (Melquist et al. 2003). In high latitudes and elevations, severe winter weather probably limits populations. In northern Canada, river otter abundance decreases with increasing latitude (St-Georges et al. 1995).

River otter density is difficult to measure, and as a result, abundance and density estimates are rarely available. Because otter distribution is usually linear along streams or shorelines, otter density is most conveniently described in terms of otters per unit length of habitat (stream or shoreline). In a mountain valley of western Idaho, reported densities of otters in different study areas ranged from one otter per 2.7 to 5.8 km, with an average of one otter per 3.9 km (Melquist and Hornocker 1983). On the Dolores River in arid southwestern Colorado, the density of translocated otters 13 months after release was one otter per 13 km (Malville 1990). Radio telemetry studies yielded density estimates of one otter per 71 to 116 ha in a Texas coastal marsh (Foy 1984), and one otter per 2.2 to 3.8 km of shoreline in coastal Alaska (Bowyer et al. 2003). In the interior west, river otters probably achieve maximum density at around one otter per 2.5 km of stream or shoreline (Melquist and Hornocker 1983, Melquist et al. 2003).

Colorado

River otters historically occupied every major river drainage in Colorado. Armstrong (1972) noted historical specimens and reliable observations from the Yampa, White, Colorado, Gunnison, and Dolores rivers in western Colorado, and from the upper and lower reaches of the Arkansas and South Platte rivers in eastern Colorado. While no historical records exist for the Rio Grande watershed in Colorado, because river otters are well documented historically in the Rio Grande in northern New Mexico (Polechla 1985), Armstrong (1972) assumed their presence in the upper reaches in Colorado as well. River otters would have historically occurred in every national forest in Colorado. Naturalists reported in the late 1800's that river otters were uncommon to rare in Colorado (Armstrong 1972), but they probably were more common prior to the fur trapping era, which began as early as the 1700's in southern Colorado and peaked statewide in 1830-1840. River otters were apparently extirpated by the early 1900's (Armstrong 1972, Fitzgerald et al. 1994), with the last record of indigenous river otters in the Yampa River in 1906 (Colorado Division of Wildlife 2003b).

The current distribution of river otters in Colorado (**Figure 3**) is likely the result of reintroductions by CDOW since 1976 into the upper Colorado River (Rocky Mountain National Park), the Gunnison River (Delta and Montrose counties), the Piedra River (Archuleta County), and the Dolores River (Dolores County). River otters reintroduced to the Green River in northeastern Utah have apparently expanded their distribution downstream into northwestern Colorado.
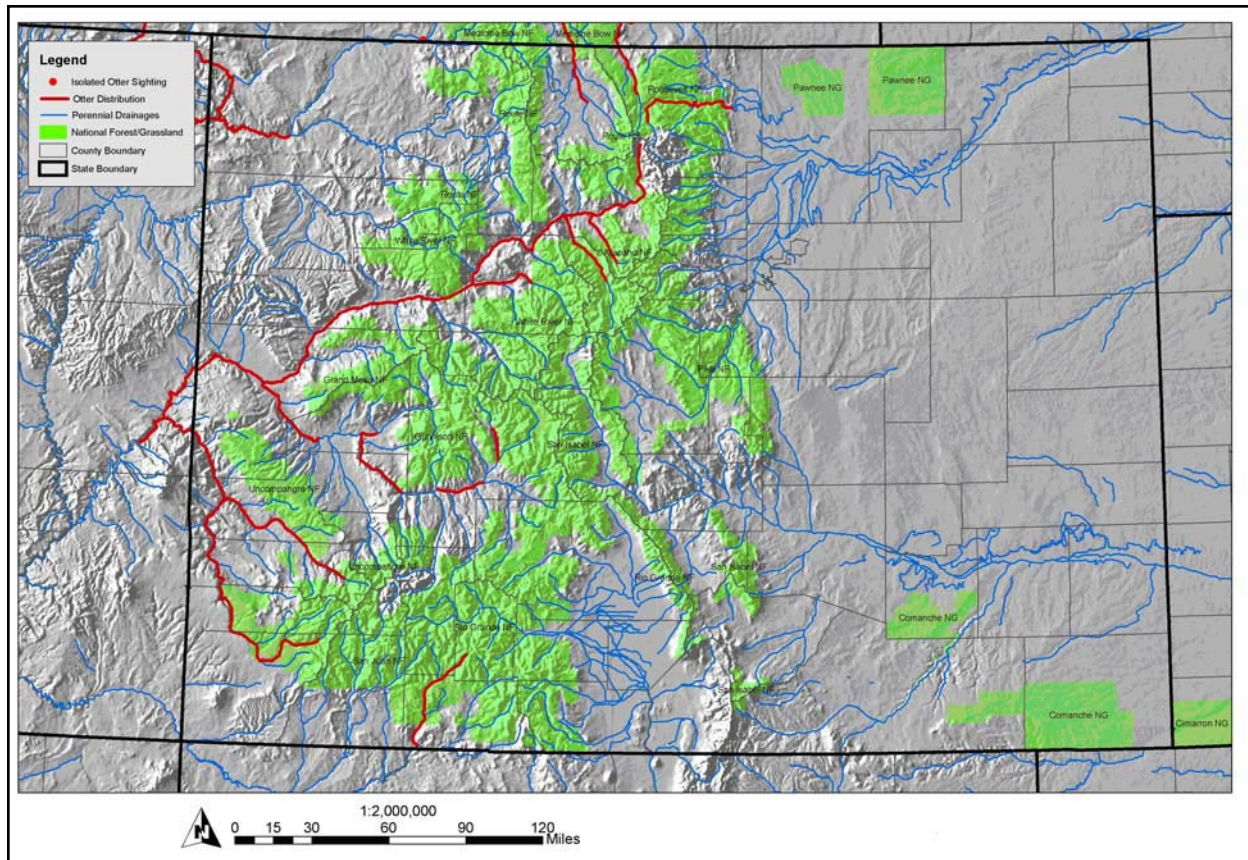
Figure 3. Estimated current distribution of river otters in Colorado.

An otter reintroduction to Cheeseman Reservoir near Denver in the 1970's was apparently unsuccessful (Colorado Division of Wildlife 2003b).

Between 1976 and 1981, 21 river otters from Newfoundland, Wisconsin, and Washington were released into the Gunnison River system at the lower end of the Gunnison Gorge National Recreation Area and the upper end of the Black Canyon of the Gunnison National Park (Colorado Division of Wildlife 2003b). River otters now inhabit the river from the upstream end of the national park downstream to the Colorado River confluence, except for a 40 km reach from the North Fork confluence to about 5 km below Delta (DePue 2002, Colorado Division of Wildlife 2003b). Otters, presumably from this population, have been seen in the North Fork Gunnison River, and regular sightings occur in the Uncompahgre River to about 8 miles south of Montrose and in large irrigation canals in the Uncompahgre Valley. A few river otters now also inhabit the Gunnison and East rivers in Gunnison County (Boyle 2003). These otters presumably moved upstream through three large reservoirs from the lower Gunnison River population.

From 1978 to 1984, 45 river otters from Washington, Wisconsin, Michigan, Virginia, and Minnesota were released on the North Fork Colorado River in western Rocky Mountain National Park (Colorado Division of Wildlife 2003b). Several recent surveys confirm that river otters now inhabit most of the North Fork Colorado River in Rocky Mountain National Park and the Arapaho-Roosevelt National Forest, including Shadow Mountain and Granby reservoirs and Grand Lake (Colorado Natural Heritage Program 2002). Sightings indicate that otters now occur along the Colorado River west to Utah, and in several major tributaries including the Fraser, Blue, Eagle, and Roaring Fork rivers, although population size and stability in these tributaries is unknown. Otters, presumably from these reintroductions, have also moved into the North Platte River in North Park and across the Continental Divide into the Poudre and Laramie rivers (Colorado Division of Wildlife 2003b).

In the Piedra River, between 16 and 24 otters (records are unclear) from Wisconsin were released from 1979 to 1983 in the San Juan National Forest upstream of the Highway 160 bridge (Colorado Division of Wildlife 2003b). A sign survey in 2002 indicated that river otters inhabit the Piedra River from Navajo Reservoir upstream at least 27 miles, and sightings

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have occurred in Navajo Reservoir and Williams Creek Reservoir. Although a river otter was observed in the Los Pinos River in the 1980's, a systematic sign survey in 2002 found no evidence of otters (Colorado Division of Wildlife 2003b).

In the Dolores River, 27 river otters (primarily from Oregon with a few from Alaska and California) were released from 1988 to 1991 near Dove Creek in Dolores County (Colorado Division of Wildlife 2003b). River otters now occur throughout the Dolores River from about 6 miles above McPhee Reservoir to the confluence with the Colorado River, including parts of the San Juan National Forest. Otters from this population have colonized the San Miguel River as far upstream as Telluride, in the Grand Mesa Uncompahgre Gunnison National Forests.

Between 1989 and 1992, the Utah Division of Wildlife Resources reintroduced 67 river otters from Alaska and Nevada at various sites along the Green River, from Flaming Gorge Reservoir to Ouray National Wildlife Refuge (Colorado Division of Wildlife 2003b). Otters now occur throughout the Green River in Colorado and probably the lower Yampa River.

Survey observations by volunteers indicate that a few river otters may be present in at least parts of the South Platte River from Denver east to the Colorado-Nebraska state line (Colorado Division of Wildlife 2003b). These otters may have originated from reintroduced populations in the upper Colorado River or from Nebraska.

Kansas

River otters historically inhabited the major rivers of Kansas, particularly in the eastern half of the state (Bee 1981). Historical distribution and abundance are unclear for the western half of the state. River otters were greatly reduced or extirpated in Kansas by the early 1900's, but currently inhabit several drainages in the eastern half of the state (**Figure 4**; Ostroff 2001). Nineteen otters from Idaho and Massachusetts were reintroduced in 1983-1984 on the South Fork Cottonwood River in Chase County (M. Peak personal communication 2003). The reintroduction has not been systematically monitored, but some otters currently inhabit the drainage. Most river otters in Kansas have likely dispersed from Missouri, where multiple reintroductions established a population of 11,000 otters by 2000 (Missouri Department of Conservation,
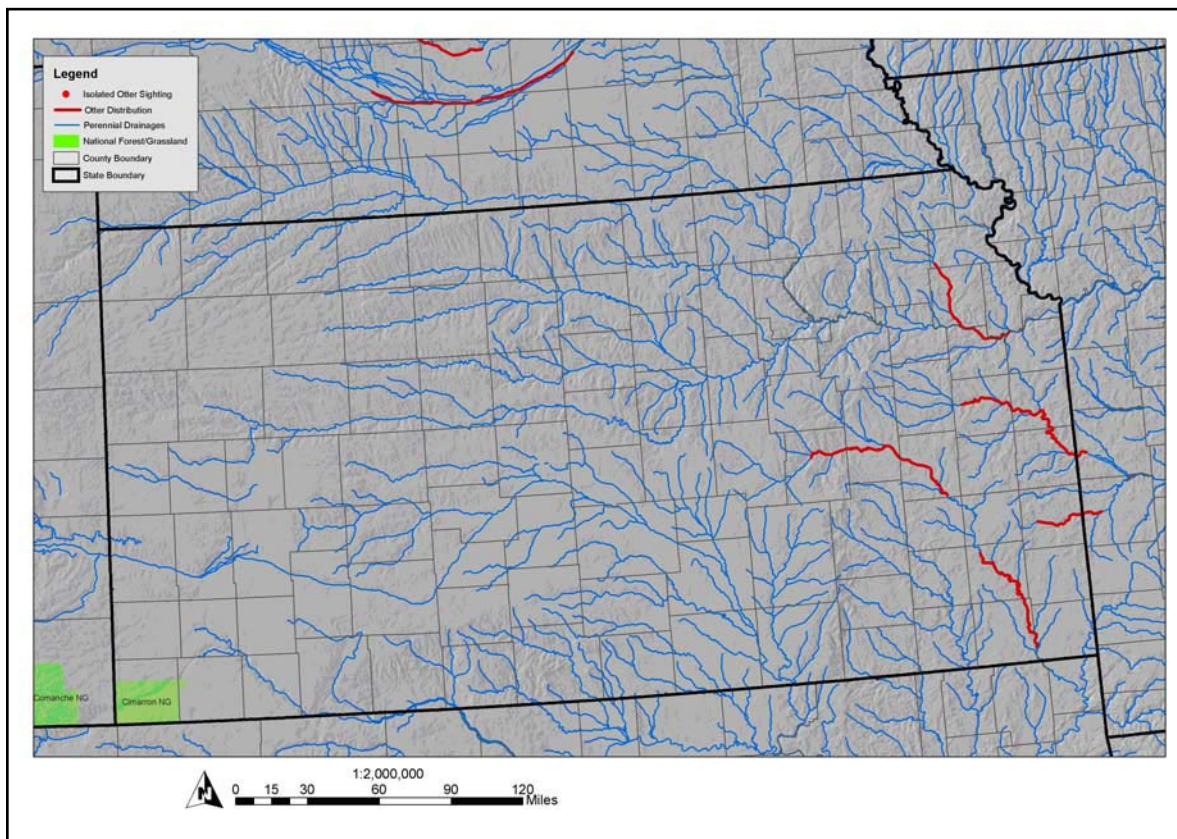
Figure 4. Estimated current distribution of river otters in Kansas.

unpublished data). River otters may also be colonizing eastern and central Kansas from reintroductions in Oklahoma and Nebraska. The nearest recent otter sightings to the Cimarron National Grassland are a few hundred miles northeast. Little suitable habitat exists in the Cimarron National Grassland area. The statewide population size is unknown, but probably exceeds 100 (M. Peak personal communication 2003).

Nebraska

River otters were historically common in all major waterways of Nebraska (Jones 1962, 1964), but they became rare by 1908 and apparently were extirpated from Nebraska shortly afterward (Jones 1964); unregulated trapping was probably the most important cause (Nebraska Game and Parks Commission 2003). Occasional sightings reported between about 1970 and 1986, mostly in the Republican River drainage, suggest that transient otters were present, but evidence of viable populations was lacking. Between 1986 and 1991, the NGPC released at least 20 otters at each of seven sites (Nebraska Game and Parks Commission 2003) including the South Loup River (Custer County), Calamus River above Calamus

Reservoir (Loup County), North Platte River above Lake McConaughy, Platte River near Kearney, Cedar River (Wheeler County), Elkhorn River (Antelope County), and the Niobrara River (Sheridan County). NGPC biologists expected river otters to expand their ranges from these release sites into suitable habitats statewide. Sightings of otters, including family groups at the release sites, along with excellent body condition of recovered carcasses, suggest that viable populations have become established in several watersheds (**Figure 5**; Nebraska Game and Parks Commission 2003). The highest quality and most extensive habitat occurs in the Platte River and tributaries, and reintroductions have been most successful there (R. Bischof personal communication 2003). No abundance estimates are available for Nebraska.

South Dakota

In South Dakota, river otters were historically common in major waterways. Turner (1974) described river otters as absent from the Black Hills region and of uncertain historical occurrence there. Grinnell (1875) speculated that river otters might occur in the Black Hills, and Turner (1974) cited accounts of river otter
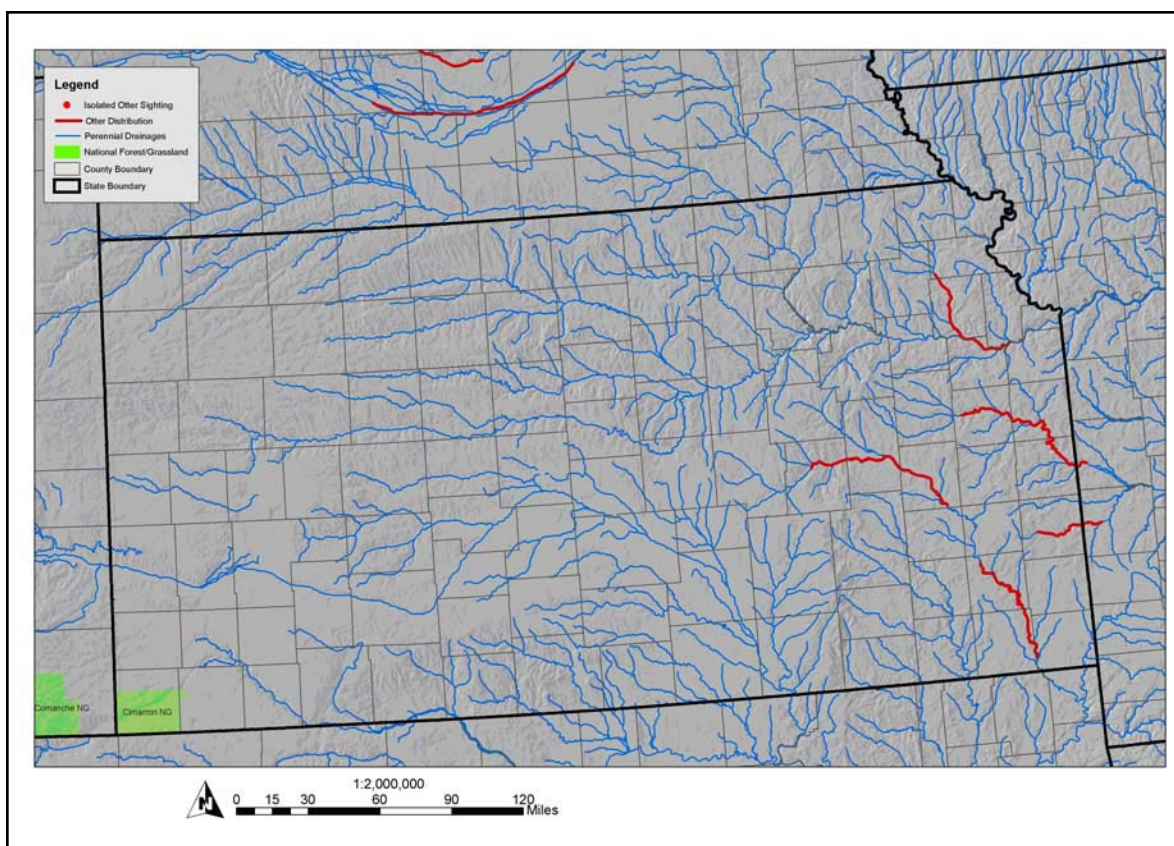
Figure 5. Estimated current distribution of river otters in Nebraska.

skins obtained in the 1800's from "west of the Black Hills". River otters were decimated by unregulated fur trapping statewide and habitat degradation in some areas, and were nearly or completely extirpated by the early 1900's.

The current known distribution of river otters in South Dakota (**Figure 6**) is mostly along the Big Sioux River near the eastern edge of the state, where the Flandreau Santee Sioux reintroduced 34 otters on tribal lands in 1998-1999. Kiesow (2003) reported that 89 percent of recent river otter sightings were east of the Missouri River and that the Big Sioux River population probably represents the only viable population in the state. Various records of river otters in other parts of the state during the last 20 years presumably represent transient or dispersing otters (Higgins et al. 2000). In 1988, a river otter reintroduced to Nebraska the previous year was trapped along Crow Creek in Buffalo County, and other reports indicate that Nebraska otters are gradually colonizing southern South Dakota (A. Kiesow personal communication). Recent sightings or trap records have occurred in Custer, Haakon, Roberts, and Union counties. No abundance estimate is available for South Dakota, but the statewide population is likely less than 100.

Wyoming

River otters historically occupied all major drainages and national forests in Wyoming, but they were subject to many local extirpations during the era of unregulated trapping (Rudd et al. 1986). Aided by the protection offered by Yellowstone and Grand Teton national parks, river otters persisted in northwestern Wyoming. Since receiving protection from trapping in 1953, river otters have reoccupied some of their former range from refugia in the northwest part of the state (Rudd et al. 1986), and possibly from remnant or reintroduced populations elsewhere.

Current distribution in Wyoming (**Figure 7**) includes most major river systems, but the extent to which all formerly occupied habitat is now inhabited is unknown. River otters occur in the Shoshone, Bighorn, and Medicine Bow national forests. Crowe (1986) reported that river otters were most common in the Yellowstone, Green, and Snake River drainages, occasionally observed in the Clark's Fork and Salt River drainages, and infrequently reported in the North Platte and Powder River drainages. River otters occur in the following counties: Albany, Big Horn, Carbon, Fremont, Hot Springs, Johnson, Lincoln, Natrona,
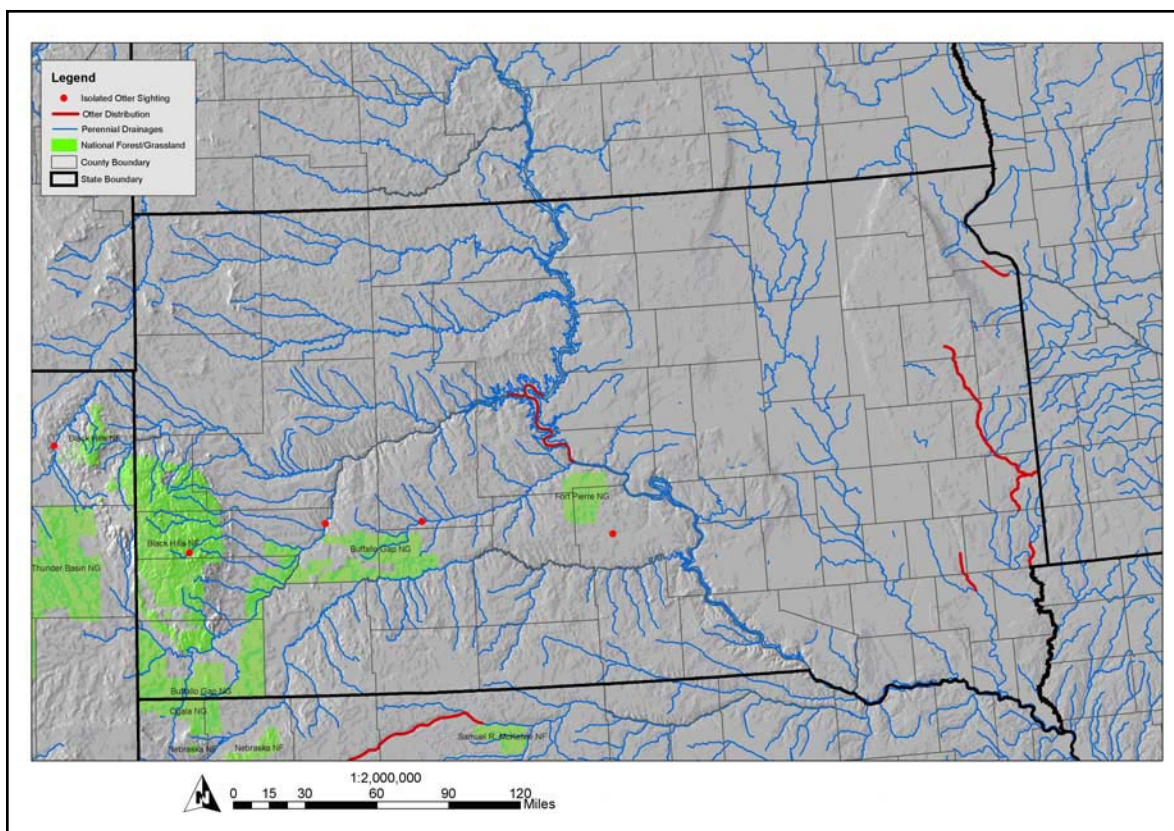
Figure 6. Estimated current distribution of river otters in South Dakota.
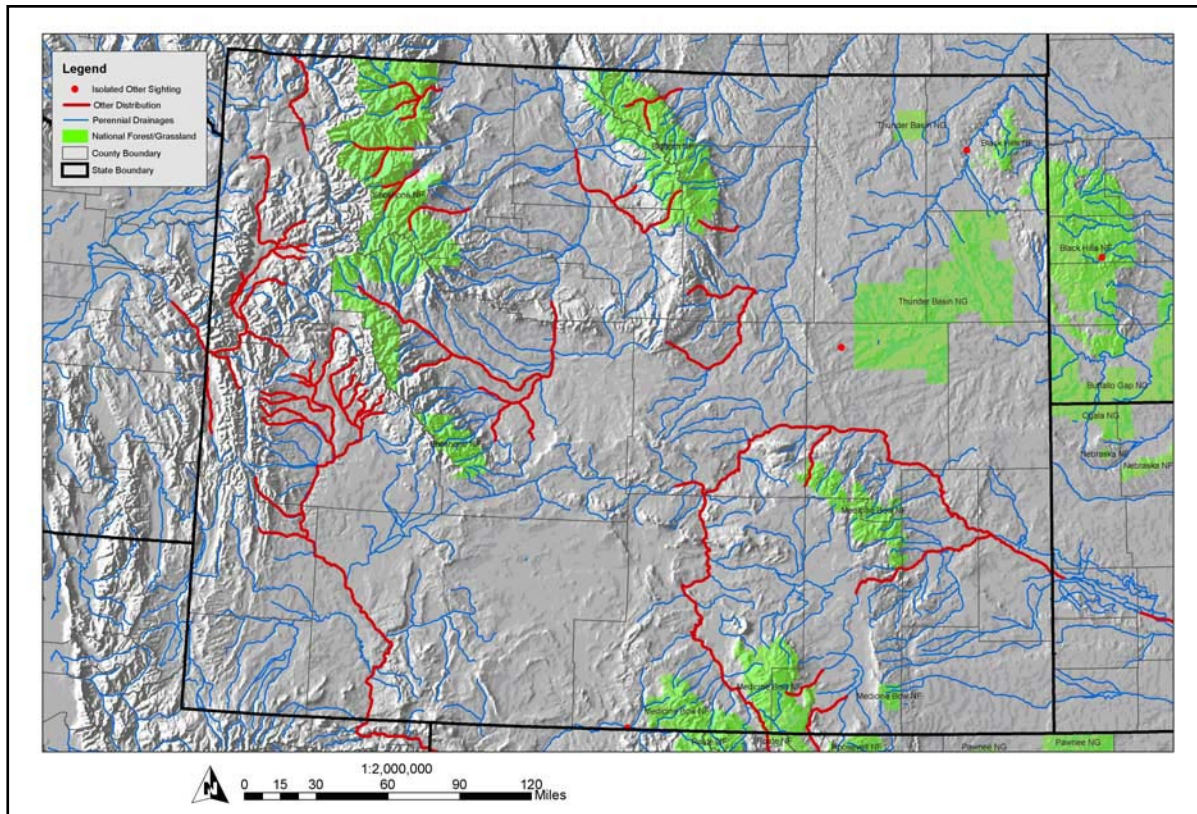
Figure 7. Estimated current distribution of river otters in Wyoming.

Park, Sheridan, Sublette, Sweetwater, Teton, and Uinta (Wyoming Natural Diversity Database 2003). No abundance estimates are available for Wyoming.

Region 2

Outside of Wyoming, river otter populations in Region 2 are best considered highly fragmented but expanding as several populations increase in size and range. River otters are highly mobile and readily disperse along waterways, and they are able to move between drainages by crossing high ridges or even mountain passes (Melquist and Hornocker 1983). Available data from Colorado and Nebraska indicate that reintroduced populations may eventually repopulate many historical ranges where adequate habitat remains and protection from excessive human-caused disturbance and mortality is afforded.

In Region 2, river otters probably have the potential for greatest density in relatively pristine reaches of lower elevation rivers on the Great Plains and at lower to middle elevations in the mountains. Little habitat exists for river otters on most of the Region 2 national grasslands and the national forests in Nebraska. In the mountains, river otter habitat quality and potential population density probably decreases at higher altitudes, with diminishing stream size and productivity and, often, increasing gradient. Much potential river otter habitat in Region 2 remains unoccupied or visited only by presumably transient otters.

Population trend

Reintroductions and management actions in recent decades have improved the conservation status of the river otter (Melquist et al. 2003). The total North American population size is unknown but probably exceeds 100,000, given the reported annual trapping harvest of up to about 30,000 river otters in the 1990's (Melquist et al. 2003), and it is believed to be stable overall (Polechla 1990). River otters are difficult to census, and estimates of population size and trend have historically been based on observations of distribution, annual fur harvest data where trapping is permitted, or monitoring methods of uncertain or low accuracy (Melquist et al. 2003). The extent of occupied range provides at least some indication of population trend. However, in areas where populations are not systematically monitored, population estimates and trends are speculative. Estimates of state population trends by state agency biologists in 1998 (Raesly 2001) are summarized in **Table 2**.

Table 2. Trend and type of populations of river otters in states within USDA Forest Service Region 2 (from Raesly 2001).

State	Population Trend	Population Type
Colorado	Stable	Reintroduced
Kansas	Stable	Native, Reintroduced
Nebraska	Stable	Reintroduced
South Dakota	Stable	Native?, Reintroduced
Wyoming	Increasing	Native

Based on the number of recent observations, Crowe (1986) reported that river otters in Wyoming might be increasing. In Colorado, more recent evidence from systematic monitoring suggests that river otters are increasing in the Colorado and Gunnison River systems (P. Schnurr personal communication 2003). Expanding populations in several watersheds in Nebraska and eastern Kansas suggest that populations may also be growing in those areas. The extent to which populations can continue to expand spatially and grow in numbers is uncertain, particularly in light of ongoing habitat degradation in some areas, increasing human populations, and increasing human demands for water.

Activity and movements

Otters are highly mobile and often move in response to shifting availability of food; consequently, home range size and location are dynamic. Reported annual home range sizes in Idaho are 31 to 58 km of waterway for adult females and 50 to 80 km for adult males (Melquist and Hornocker 1983). In Rocky Mountain National Park, annual home ranges of otters of both sexes ranged from 5 to 71 km, with an average of 32 km (Mack 1985). On the Dolores River, Colorado, home ranges of otters during the first year after translocation varied from 9 km in winter to 22 km in summer, with spring and fall home range sizes intermediate (Malville 1990). Male home ranges are usually larger than those of females. Both sexes exhibit inter- and intrasexual overlap in home ranges, and home ranges tend to shrink in winter and exhibit less overlap (Melquist and Hornocker 1983, Mack 1985, Reid et al. 1994b, Bowyer et al. 1995). "Activity centers" (Melquist and Hornocker 1983) are areas within the home range where river otters focus activity during certain periods. Such areas provide adequate shelter, abundant food, and minimal disturbance (Melquist and Dronkert 1987); examples are large logjams with spawning salmon in Idaho (Melquist and Hornocker 1983) and deep river pools with abundant crayfish and beaver bank dens in Colorado (Malville 1990).

River otters are more social than most mustelids. In freshwater systems, the most typical social group consists of an adult female and her recent offspring (Melquist and Hornocker 1983). In coastal marine systems, males commonly form groups of up to 21 individuals (Shannon 1989, 1991, Blundell et al. 2002a); this apparently aids in cooperative foraging for schooling fish (Blundell et al. 2002a). In freshwater systems, males may also occasionally form groups (Larivière and Walton 1998), and groups of unrelated juveniles are occasionally observed (Melquist and Hornocker 1983, Shannon 1989). River otter groups hunt and travel together and use the same resting sites, latrines, and dens (Shannon 1989, Beckel 1990, Reid et al. 1994b, Shannon 1989). Groups of mothers and juveniles usually break up between November and March, and juveniles often permanently disperse at age 12 to 13 months (Melquist and Hornocker 1983).

Otters forage both in groups and singly. Behavior interpreted as cooperative foraging has been observed in Pennsylvania (Serfass 1995) but rarely observed elsewhere (for example, Beckel 1990). Even without direct cooperation, foraging in groups appears to increase forage efficiency and diet quality in coastal Alaska river otters (Blundell et al. 2002a).

River otters are active year-round, but in general, they are more active at night and during crepuscular hours (Larivière and Walton 1998); daily activity peaks for river otters in Idaho were around midnight and dawn (Melquist and Hornocker 1983). Daily activity also varies with season, at least in the Rocky Mountains. River otters in Rocky Mountain National Park, Colorado (Mack 1985) and in Idaho (Melquist and Hornocker 1983) are more diurnal in the winter.

Melquist and Hornocker (1983) found that Idaho river otters typically moved 2 to 5 km daily, with movements up to 42 km in one day. Similar average daily movement patterns were reported for river otters in Alberta lake country (Reid et al. 1994b) and for

otters during the first year after translocation in the Dolores River, Colorado (Malville 1990). Yearling males move somewhat more than females in all seasons. Family groups and individual otters tend to move less in winter.

River otters do not migrate (Larivière and Walton 1998), but they may emigrate because of food shortages or environmental conditions (Jackson 1961). Dispersal in river otters appears to be an inherent trait unrelated to population density (Melquist and Hornocker 1983). Many, but not all, river otters disperse when about 12 to 13 months old. Some leave the watershed, some move to a different part of the same watershed, and some merely expand their natal home range to include additional area. In coastal Alaska, dispersal distances ranged from 15 to 90 km (Blundell et al. 2002b). In general, river otters remain close to water, but occasionally they will go overland to shortcut meanders or detour falls; they will move between major drainages, occasionally even traversing mountain passes (Melquist and Hornocker 1983).

Habitat

Rangewide, river otters inhabit almost every kind of aquatic habitat, including marine coasts, lakes, marshes, reservoirs, and streams (Toweill and Tabor 1982, Larivière and Walton 1998). They inhabit water bodies and riparian areas within a broad range of ecosystems from semi-desert shrubland to montane and subalpine forest. The primary habitat requirement for river otters is permanent water with abundant fish or crustacean prey and relatively high water quality.

In the interior western United States, river otters most often inhabit stream-associated habitats (Melquist and Hornocker 1983, Mack 1985, Bradley 1986), but lakes, reservoirs, beaver ponds, and floodplain wetlands may occur within seasonal home ranges. Otters prefer valley streams to mountain streams. In mountainous areas, headwater streams or stream reaches are often characterized by high gradient and low productivity and, therefore, do not provide quality habitat for river otters (Melquist and Hornocker 1983, Dubuc et al. 1990). In Nevada, river otters favored streams with low gradient, high meander ratios, and multiple channels (Bradley 1986). In montane valley habitat in Rocky Mountain National Park, Colorado, Mack (1985) estimated that rivers, small streams, and beaver ponds contained 42, 4, and 54 percent, respectively, of the total energy available to river otters in the form of fish prey.

Because of their high mobility and low densities, river otters require relatively long reaches of streams and rivers. They will occupy lakes and reservoirs, as long as shoreline cover and food resources are adequate (Melquist and Hornocker 1983), and river otter presence has been reported in several large lakes and reservoirs in Colorado (Colorado Division of Wildlife 2003b). In Maine, river otter use of watersheds is positively associated with average shoreline diversity (Dubuc et al. 1990). Complexity of river and lake shorelines provides greater areas of shallow water and wetlands, which provide shallow water habitats for otter prey, including slower-swimming fish, amphibians, reptiles, and invertebrates. Use of marshes may vary with the season. In Florida, river otters will move during the dry season from freshwater marshes to permanent ponds where water is available and food is more concentrated (Humphrey and Zinn 1982).

The physical habitat attribute most important to river otters besides water is riparian vegetation, which provides security cover when they are feeding, denning, or moving on land. Riparian vegetation also enhances otter habitat by stabilizing banks (which reduces soil erosion and protects water quality), contributing nutrients and invertebrates to aquatic systems, providing shading for fish habitat, and encouraging beaver activity. Another essential habitat component is structural diversity and complexity provided by objects such as fallen trees, logjams, stumps, undercut banks, and rocks (Melquist and Dronkert 1987). Structural complexity depends on surface geology, presence of trees in riparian zones, and beaver activity.

The importance of cover along waterways for river otter habitat is clear. If riparian vegetation is lacking, rock piles or similar physical structures may provide such cover. River otters generally avoid areas where cover is lacking, such as reservoir shorelines with little vegetation or structural cover, even if food is abundant (Melquist and Hornocker 1983). River otters scent mark profusely with feces, urine, and anal gland secretions (Melquist and Hornocker 1983). Physical structures in and near waterways are extensively investigated and used by river otters for latrine sites important for olfactory communication. Important latrine sites include points of land, the base of large conifers, beaver bank dens and lodges, isthmuses, mouths of permanent streams, and logjams or rocks protruding from the water (Melquist and Hornocker 1983, Newman and Griffin 1994).

River otters make considerable use of beaver bank dens, dams, and lodges for latrine sites, dens, and resting sites (see Community Ecology section). Beaver bank dens are especially important sites, used in 31 percent of over 1,300 observations in Idaho (Melquist and Hornocker 1983). River otters rest in dens, choosing sites opportunistically when the need arises. On larger rivers confined by canyons and lacking side channels that beavers can impound, beavers excavate bank dens that river otters use extensively. In the Dolores River, Colorado, river otters strongly preferred deep pools that also contained a high number of beaver bank dens and in-stream boulders protruding above the water surface (Malville 1990). Almost all resting sites were beaver bank dens, and den complexes with many openings both above and below water were preferred. Other den sites reported from the northern Rockies, Alberta, and the eastern United States include red fox (*Vulpes vulpes*) burrows, beaver or muskrat lodges, dense riparian vegetation, log jams, snow and ice caves, brush piles, and talus (Liers 1951, Melquist and Hornocker 1983, Reid et al. 1994b). Reintroduced river otters in Pennsylvania were also observed using hollow trees or logs, undercut banks, rock formations, and flood debris (Serfass and Rymon 1985).

In areas with severe winters, winter ice presents a strong constraint on river otter habitat use. In boreal forests of Alberta, cold temperatures and the presence of ice reduce foraging area, prey availability, and presumably foraging success (Reid et al. 1994b). River otters in winter show substantial range contraction especially by adult males, less home range overlap with other individuals, and more solitary behavior. In Alberta, otters in winter are mostly confined to lakes that provide suitable shoreline habitat for beaver bank dens or lodges. These features provide otters with shelter and access to foraging areas beneath the ice (Reid et al. 1994b). In areas of Region 2 with hard winters, winter habitat availability probably limits river otter abundance, and otters depend more on beaver-modified environments. Ice can provide cover in areas where it otherwise is lacking, but presence of at least some open water in winter is a critical habitat element. River otters make heavy use of openings in ice, and they may excavate passages in beaver dams to access open water (Hamilton 1943, Reid et al. 1994b).

Food and feeding habits

Fish form most of the river otter's diet rangewide, and the presence of fish in suitable quantity typically constitutes an essential habitat component. River otters will also take crustaceans, mollusks, insects, birds, and mammals, occasionally in abundance but more often opportunistically (Knudsen and Hale 1968, Reid et al. 1994a, Melquist et al. 2003). Fish remains were present in all scats examined from Grand County, Colorado (Mack 1985) and 92 percent of scats in northeastern Alberta (Reid et al. 1994a). In some areas and seasons, fish constitute virtually the entire diet (Greer 1955, Toweill 1974, Melquist et al. 1981). Fish species are taken in proportion to their availability, which is related both to fish abundance and the relative ease of each species' detection and capture (Toweill and Tabor 1982, Melquist and Hornocker 1983). Slower-swimming and less agile fish such as suckers (Catostomidae), catfish (Ictaluridae), sculpin (Cottidae), and minnows (Cyprinidae) are usually favored (Stenson et al. 1984, Serfass et al. 1990, Reid et al. 1994a). In the Dolores River, Colorado, channel catfish (*Ictalurus punctatus*), carp (*Cyprinus carpo*), and bluehead suckers (*Catostomus discobolus*) are the most common fish consumed by river otters (Malville 1990, Colorado Division of Wildlife 2003b). River otters in Rocky Mountain National Park mostly consumed introduced trout (*Salmo* and *Oncorhynchus* species) and native suckers (Mack 1985). In an Idaho montane valley, the three most important fish species in otter diets were kokanee salmon (*O. nerka*), mountain whitefish (*Prosopium williamsoni*), and largescale sucker (*C. macrocheilus*) (Melquist and Hornocker 1983). Salmonids and suckers taken in both areas were mostly adult fish over 30 cm in Idaho and over 20 cm in Rocky Mountain National Park. Apparently, river otters prefer adult fish because they are less maneuverable and less able to find hiding cover (Erlinge 1968). River otters sometimes move into small streams or mountain lakes to take advantage of trout or salmon spawning runs (Melquist and Hornocker 1983, Reid et al. 1994a).

In some cases, amphibians (mostly frogs) and crustaceans (mostly crayfish) make up important parts of the diet (Sheldon and Toll 1964, Knudsen and Hale 1968, Griess and Anderson 1987, Reid et al 1994a); crayfish are especially important in some areas of Region 2. Crayfish can be more important than fish in river otter diets in places where crayfish are abundant, such as lower elevation rivers in southwestern Colorado (Malville 1990, DePue 2002) and some California marshes (Grenfell 1974). Malville (1990) observed river otters rolling submerged rocks to expose crayfish. Mollusks are common in river otter diets in some areas, particularly lake regions and marine coasts (Melquist et al. 2003).

Large insects form an important segment of the river otter's diet in warmer months. Insects were the

second most frequent diet item of river otters in Alberta (Reid et al. 1994a), and included aquatic beetles and dragonfly nymphs. In Idaho, river otters actively sought insects 2 to 8 cm in length, including aquatic beetles and stonefly nymphs (Melquist and Hornocker 1983).

River otters will also take reptiles, birds, and fruits opportunistically (Wilson 1954, Greer 1955, Hamilton 1961, Morejohn 1969, Verbeek and Morgan 1978, Gilbert and Nancekivell 1982). Birds in the diet are often waterfowl, especially broods and molting adult ducks taken in summer in lake habitats (Reid et al. 1994a). Waterfowl can be a fairly important part of the diet in some areas (Toweill and Tabor 1982), but in Region 2 this would only be likely in large wetlands.

Rarely, river otters will prey on various small mammals. Muskrats were the most common mammal prey in Idaho scats (Melquist and Hornocker 1983), primarily in marsh areas. Beaver remains have been occasionally reported in river otter scats (Green 1932, Reid et al. 1994a). While river otters sometimes inhabit beaver dens simultaneously with beavers (Melquist and Hornocker 1983, Malville 1990), most studies have reported no beaver remains in scats despite considerable presence of beavers in the area.

Fish and other prey are taken with a quick lunge from ambush, or more rarely after a prolonged chase (Park 1971). River otters can remain underwater up to nearly 4 minutes (Harris 1968), swim up to 11 km per hr, dive to nearly 20 m, and travel up to 400 m underwater including under solid ice (Hamilton 1943, Jackson 1961, Park 1971). Several individuals may cooperate to capture fish (Serfass 1995). Small fish are eaten at the surface, but large fish are taken to shore for consumption (Park 1971, Chanin 1985).

In Idaho, river otters typically forage where fish congregate and seek cover, such as overhanging banks and log jams in shallow, fast streams, log jams in deep pools, and boat docks or floating wood in large lakes and reservoirs (Melquist and Hornocker 1983). In reservoirs with many slow-moving fish, river otters often forage along shorelines and capture slow-moving fish by direct pursuit. River otters were seen probing mud bottoms in shallow backwaters and oxbows for small fish and beetles.

River otters are opportunistic feeders, taking whatever prey is most abundant and most catchable. Food availability is a prime factor in determining otter movements and habitat use (Melquist and Hornocker 1983). River otters tend to forage in a pool, stream reach, lake, or pond until food availability is reduced, then move to other sites. Otters will move large distances to capitalize on seasonally abundant food resources. In northern or high elevation areas where lakes and rivers freeze, otter diets are less diverse in the winter and reflect the otter's dependence on small lakes, bog ponds, and beaver ponds (Reid et al. 1994a).

The biology of fish, the otter's primary prey, is complex, and fish populations respond to a number of physical and biological factors in the aquatic environments they inhabit and to factors in the surrounding terrestrial landscape (Hart and Reynolds 2002). In Region 2, most rivers, streams, and lakes have an assemblage of native and non-native species. Primary factors affecting species diversity and abundance of fish in Region 2 include water volume (including human alteration in volume and flow), temperature, turbidity, and pollution; stream size, gradient, and structural cover; riparian habitat factors; and fish introductions and harvest by humans (Abell 1999, Hart and Reynolds 2002).

Crayfish, the other significant prey item for river otters in Region 2, include native species and species introduced into reservoirs and tailwater fisheries for fish food. Crayfish are sensitive to changing water temperatures. Most species can tolerate considerable turbidity, but water pollution and sedimentation may affect planktonic and benthic invertebrate crayfish prey (Holdich 2002).

Breeding habits

River otters are polygynous (Melquist et al. 2003). Throughout their range breed from December to April (Larivière and Walton 1998), but in Region 2 they probably breed in March and April (Melquist and Hornocker 1983, Fitzgerald et al. 1994). Females are in heat for 42 to 46 days (Hamilton and Eadie 1964), during which time the males follow scent trails of the females (Fitzgerald et al. 1994). Copulation lasts 16 to 73 minutes and may occur in water or on land (Liers 1951, Shannon 1991). True gestation lasts 61 to 63 days, but because the fertilized egg does not implant in the uterus for 8 months or more, the time between copulation and parturition may reach 10 to 12 months (Liers 1951, Hamilton and Eadie 1964). Delayed implantation may not always occur in some southern populations (Melquist and Dronkert 1987), but it probably is the rule in Region 2. Young are born between February and April (Hamilton and Eadie 1964, Melquist and Hornocker 1983). Females retire to secluded locations to give birth and to rear young, generally using dens of other aquatic

mammals, especially beaver bank dens (Melquist and Hornocker 1983). Occasionally natal dens may be up to a few hundred feet from water (Melquist and Dronkert 1987). Breeding may take place anywhere in a female's home range, and natal den availability is probably not limiting to river otter populations as long as overall den sites are reasonably abundant.

Litter size is usually one to three (Hamilton and Eadie 1964, Tabor and Wight 1977, Docktor et al. 1987), occasionally up to five (Park 1971), and averages slightly less than three (Melquist et al. 2003). No geographic variation in litter size is apparent. Young are born fully furred, blind, and toothless (Larivière and Walton 1998). Females nurse their young and provide solid food; males do not provide parental care (Shannon 1989). Kits take their first solid food at 9 to 10 weeks (Liers 1951), and are fully weaned by 12 weeks. Juveniles remain with females until they are 37 to 38 weeks old, during which time females provide food for their young and teach them to hunt (Shannon 1991). Quiet waters such as beaver ponds, marshes, and backwater sloughs appear to be important areas for family groups with young pups learning survival skills (Melquist and Hornocker 1983). In Idaho, young dispersed in April and May at 12 to 13 months of age, and they dispersed up to 200 km at an average rate of 3.5 to 3.8 km per day (Melquist and Hornocker 1983). Both sexes reach maximum weight and length at age 3 to 4 years (Melquist and Hornocker 1983).

Demography

Genetic variability of river otters across their current North American range is lower than average for mammals as a whole, but comparable to other mustelids and mammalian carnivores (Serfass et al. 1998). Large home ranges and an ability to disperse long distances (Melquist and Hornocker 1983) tend to encourage gene flow among otter populations. However, population bottlenecks caused by large reductions in abundance in some areas of North America are a concern (Serfass et al. 1998).

Genetics

Genetic variability among Region 2 river otter populations is unknown. In Wyoming, the only state with primarily native populations, the presumed population bottleneck in the early 1900's may have reduced genetic variability. Western Wyoming otter populations are probably in contact with large river otter populations in Montana and Idaho and, thus, gene flow may be less of a concern for Wyoming populations.

In all other Region 2 states, otter populations are largely or entirely the result of reintroductions from at least 10 states and provinces over a wide range of North America. Most reintroduction sites received otters from two or more states or provinces. Consequently, the genetic makeup of these populations likely reflects the geographic origins of the founding animals, as well as possible influences of bottleneck effects, interaction with remnant or immigrant indigenous otters, and integration with other transplanted populations as they expand and come into contact.

Some reintroduced populations may remain small and isolated, such as the Piedra River population in the San Juan National Forest in southwestern Colorado, and perhaps some Nebraska populations isolated by lengthy reaches of unsuitable habitat. Small populations face increased risks from genetic drift, excessive homozygosity, and stochastic environmental and disease factors. Periodic augmentation of small, isolated populations from outside sources may be necessary to increase genetic variability.

The effects of local extirpations, the potential for natural recolonization, and the need for reintroductions all require an understanding of the influence of social structure, mating system, and sex-biased dispersal on genetic variation and gene flow among populations. Genetic relatedness (kinship) had no effect on social organization or spatial relationships among coastal marine river otters in Alaska (Blundell et al. 2004).

Life history characteristics

Sex ratios in free-ranging populations of river otter approximate 1:1. Male:female ratios of river otters trapped in 10 northeastern states varied from 0.6:1 to 3.3:1 (Chilelli et al. 1996). Reported sex ratios in New York were 1.3:1 (Hamilton and Eadie 1964), and in Idaho 1.1:1 (Melquist and Hornocker 1983). It is unknown whether differences in trapability between the sexes exist and, therefore, inject bias into sampling efforts.

Females usually do not mate until age 2, occasionally at age 1 (Hamilton and Eadie 1964). Reported breeding rates of 2-year-old females range from 20 to 55 percent, and not all females may breed every year (Toweill and Tabor 1982). Pregnancy rates seem to vary between the Pacific Northwest and the rest of North America. In British Columbia, 55 percent of 2-year-old females and 91 percent of 3-year-olds were pregnant (Stenson 1985); in Oregon, 99 percent of adult females were judged to be pregnant (Tabor

and Wight 1977). However, various authors indicate that pregnancy rates of adult females in the Midwest, Northeast, and Southern United States range from about 50 to 60 percent. These differences most likely relate to differences in environmental factors, particularly habitat conditions, prey availability, and perhaps population density (Melquist and Dronkert 1987).

In Region 2, breeding rates are unknown. Because trapping harvest does not occur in Region 2, carcasses are seldom available for examination to determine breeding rates. However, Region 2 populations probably exhibit breeding rates similar to other interior populations. Males are sexually mature at age 2 (Hamilton and Eadie 1964), but some males may not successfully reproduce until age 5 or older (Liers 1951, 1958).

Litter size is usually one to three (Docktor et al. 1987, Hamilton and Eadie 1964, Tabor and Wight 1977) and averages slightly less than three (Melquist and Dronkert 1987). Recruitment in Oregon was estimated at 1.14 young females per adult female in autumn (Tabor and Wight 1977).

Annual survival rates in Oregon were 68, 46, and 73 percent for age classes 0, 1, and 2-11, respectively

(Tabor and Wight 1977). Various terrestrial predators may kill river otters, but most mortality is human-caused and includes legal and illegal trapping, illegal shooting, road-kills, and accidental captures in fish nets or set lines (Jackson 1961, Melquist and Hornocker 1983). Reported accidental deaths include crushing by ice flows (Serfass and Rymon 1985) and shifting rocks (Melquist and Hornocker 1983). Starvation following tooth damage has been observed (Serfass and Rymon 1985). Survival up to 14 years of age has been documented for free-ranging river otters, and captive otters have lived for 25 years (Stephenson 1977, Melquist and Dronkert 1987). No long-term studies of river otter population dynamics have been carried out, and turnover rates of populations are unknown (Fitzgerald et al. 1994).

Population matrix analysis

Life cycle graph and model development: Matrix demographic models provide a means to assess the critical transitions in life history cycles. We created a life cycle graph for river otter that comprised four stages (**Figure 8**), and we formulated a matrix projection model with a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001).
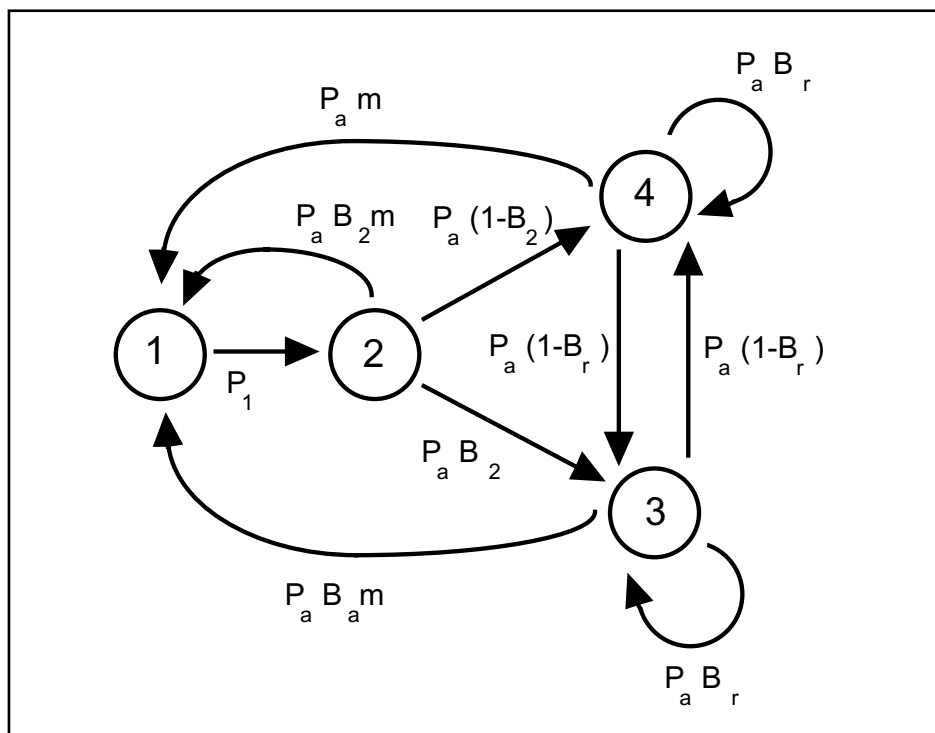
Figure 8. Life cycle graph for the river otter. Stage 1 and stage 2 are age-specific (first and second-year individuals). Stage 3 represents "off-year" females that have a low (25 percent) probability of breeding, and stage 4 represents "off-year" females that definitely breed. Following the "off-year," all females again breed in stage 3. We also assume that only 5 percent of second-year females breed, and that those females then move to the "off-year" stage 4.

Here we present a summary of the model results; the complete technical analyses are shown in the **Appendix**. Model inputs (vital rates such as survival and fertility) are shown in **Table A1**. Stage 1 represents females in their first year, with "breeding" (i.e., giving birth) probability equal to 0 (Melquist et al. 2003). Stage 2 represents second year females, with breeding probability equal to 0.05. Births by second-year females have occasionally been reported, but most females do not reach sexual maturity until their second year, giving birth in their third year because of delayed implantation (studies reviewed by Toweill and Tabor 1982, Melquist et al. 2003). Stage 3 represents females that bred in the previous year. Stage 4 represents females in at least their third year that did not breed the previous year. After first breeding, females generally alternate between Stage 3 and Stage 4. Stages 3 and 4 in the life cycle graph address the fact that the birth interval for otter females varies from one to two years (reviews by Toweill and Tabor 1982, Melquist and Dronkert 1987, Melquist et al. 2003). No data on birth intervals are available from otters in Region 2 states. High pregnancy rates of adult females reported for otter populations subject to trapping harvest in Oregon (99 percent; Tabor and Wight 1977) and Missouri (about 90 percent; Missouri Department of Conservation, unpublished data) indicate that most females in those populations bred every year. Other studies in the northeastern and southern United States reported near 0 to 25 percent of females giving birth in consecutive years (Toweill and Tabor 1982). We selected a conservative probability for breeding in consecutive years of 0.25.

Sensitivity analysis: First, we conducted a sensitivity analysis. Sensitivity is the effect on the population growth rate (λ) of an absolute change in the vital rates (i.e., survival and fertility). The rate for which λ was most sensitive was female adult survival (71 percent of total sensitivity). First-year survival sensitivity was 15 percent of the total, and fertility sensitivity summed for all stages was 13 percent of the total. We conclude from the sensitivity analysis that survival of adult females is the most important vital rate transition for population viability.

Elasticity analysis: Next, we conducted an elasticity analysis. Elasticities help resolve a problem of scale that can complicate conclusions drawn from the sensitivity analysis. Because survival rates and fertility rates are measured on different scales, interpreting the results of a sensitivity analysis can be somewhat misleading. Elasticities have the useful property of summing to 1.0. Elasticity analyses for the river otter conclude that λ was most elastic to changes

in female adult survival, summed for Stages 2 through 4 (67 percent of total elasticity), followed by first-year survival (16 percent of total) and fertilities summed for all female adult stages (16 percent of total). The results of the elasticity analysis, consistent with the sensitivity analysis, indicate that female adult survival is the most important population characteristic for population viability.

Stochastic model: Finally, we constructed a stochastic model to predict the effect of environmental variation on λ. Stochasticity was incorporated by varying different combinations of vital rates or by varying the amount of stochastic fluctuation. The stochastic model produced two major results. First, altering the adult survival rate produced a much greater change in λ than altering either first-year survival rate or fertility rates. Second, high-amplitude stochasticity has a negative effect on λ, despite the fact that average vital rates remain the same. These results indicate that river otter populations are relatively tolerant of year-to-year fluctuations in production of offspring or first-year survival, but they are more vulnerable to fluctuations in adult survival.

Summary of conclusions from river otter matrix projection models:

❖ Sensitivity analysis indicated that λ was most sensitive to absolute changes in adult survival; first-year survival sensitivity and fertility sensitivity summed for all stages were lower.

❖ Elasticity analysis indicated that λ was most elastic to changes in adult survival, followed by first-year survival and fertilities summed for all adult stages.

❖ Stochastic simulations testing variations in vital rates showed that river otter populations are most vulnerable to changes in adult survival, and they are vulnerable to high-amplitude fluctuations in adult survival rates even when the average adult survival remains unchanged.

❖ The three analyses were consistent in identifying adult survival rate as the most important population characteristic for maintaining population viability; the stochasticity analysis further identified a vulnerability of river otter populations to year-to-year fluctuations in adult survival.

Limiting factors

The extent to which river otter social behavior limits populations is unknown. In marine coastal environments of Prince William Sound, Alaska, natal dispersal rates for river otters were less than 10 percent for both sexes (Blundell et al. 2002b). Natal dispersal distances were bimodal, with most males and some females moving 16 to 30 km but some females dispersing 60 to 90 km. However, evidence of breeding dispersal was documented for 30 percent of adult males that either shifted or expanded their home ranges during the breeding season. While the "effective dispersal" (i.e., resulting in reproductive success) could not be assessed, other genetic evidence indicated that breeding dispersal by adult males was an important contributor to gene flow between adjacent populations (Blundell et al. 2002b).

The dispersal ability of river otters contributes to population recovery and expansion, as long as large areas of suitable habitat remain. However, fairly strict habitat requirements, relatively low fecundity, and long life spans make river otter populations vulnerable to habitat alterations and can limit the speed at which impacted populations can recover (Melquist and Dronkert 1987).

In Region 2, the primary limiting factors for river otters are habitat-related. Large areas of river habitat have been degraded by water depletions and water development, decline in water quality, loss of riparian vegetation, and heavy human settlement. These areas mostly occur beyond USFS lands, in valleys where private lands dominate. However, riparian vegetation degradation has also occurred on some federal lands from livestock grazing and other land uses. Observations from river otter monitoring in Colorado (DePue 2002, Boyle 2003) suggest that river otters avoid or seldom use river reaches that no longer support suitable riparian vegetation and are heavily impacted by agriculture or urban development, despite food availability in the disturbed reaches. Melquist and Hornocker (1983) reported similar observations in Idaho.

Water development projects for agriculture and increasingly for urban development that deplete or modify natural flow regimes can also reduce habitat and prey availability for otters. For example, agricultural diversion of the Dolores River at McPhee Reservoir in the San Juan National Forest has reduced tailwater flows to about 10 cfs in recent summers. This reduction may exceed the minimum flow required to sustain populations of large fish and adequate pool volume for otters. Flow reduction and changes in the natural hydrograph may also have other long-term consequences for aquatic and riparian ecosystem health. Growth of human populations, particularly rapid in parts of Colorado, is increasing urban and suburban development pressure and recreational use along rivers, and is likely to cause further otter habitat degradation and fragmentation. These habitat losses impede the ability of recovering river otter populations to expand and may limit some small populations to nonviable size.

Community ecology

River otters are top-order carnivores that inhabit many kinds of aquatic systems. Key community relationships are summarized in the envirogram presented in **Figure 9**.

Predators

River otters in the interior west have no natural predators when they are in water, but on land or ice, they are more vulnerable. Bobcat (*Lynx rufus*), mountain lion (*Felis concolor*), coyote (*Canis latrans*), domestic dog (*C. familiaris*), gray wolf (*C. lupus*), red fox, and bald eagle (*Haliaeetus leucocephalus*) are predators present in Region 2 that have been reported to kill river otters (Melquist and Hornocker 1983, Mach 1985, Melquist and Dronkert 1987, Route and Peterson 1991, Melquist et al. 2003). An unverified report exists of black bear (*Ursus americanus*) predation on river otter in Alaska (Home 1982).

Competitors

Competition for food with other animals appears low. Mink are typically sympatric with river otters in Region 2, and the ecological niches occupied by mink and river otter partly overlap. However, differences in size, morphology, feeding habits, and foraging strategies minimize competition between the two species in Idaho (Melquist et al. 1981). In Alaska, otters and mink inhabiting marine shorelines show niche separation through resource partitioning related to each species' swimming abilities (Ben-David et al. 1996). Competitors for crayfish, an important diet item in western Colorado and southwestern Wyoming, include raccoon (*Procyon lotor*), skunk (*Mephitis* and *Spilogale* sp.), mink (*Mustela vison*), herons (Ardeidae), and predaceous fish, particularly trout. Raccoon and skunk densities often increase with human settlement, but the extent to which raccoons or other animals can deplete crayfish populations is unknown.

WEB			CENTRUM
N	2	1	

RESOURCES

Forest resource management

Riparian livestock grazing

Logging

Wildfire incidence

Topography

Elevation

Precipitation

Beavers

Riparian vegetation

Shoreline rocks

Shoreline woody debris

Instream rocks

Instream woody debris

Rivers, streams, lakes, wetlands

Den, rest, feeding, latrine sites

Nutrients from fish, invertebrates

River/Lake volume

River seasonal flow

Irrigated agriculture

Human density

Water quality

Fish predators

Fish stocking

NORTH AMERICAN RIVER OTTER

PREDATORS

Diseases

Alternate prey

Den, rest sites

Riparian vegetation

Dogs

Mountain lion, coyote, wolf

MALENTITIES

Trapping regulations

Economic growth

Fur prices

Scenery, rural amenities

Human density

Beaver trapping effort

Road proximity to streams, lakes

Trappers (incidental take)

Road kill, shooting, human disturbance

Parasites and disease

Melquist et al. (2003) reviewed river otter parasites and diseases. River otters host numerous kinds of endoparasites including nematodes (Hoberg et al. 1997), cestodes (Greer 1955), trematodes and sporozoans (Hoover et al. 1984), and acanthocephalans (Hoberg et al. 1997, Hoover et al. 1984). Ectoparasites include ticks (Eley 1977, Serfass et al. 1992), sucking lice (Kim and Emerson 1974), and fleas (Serfass et al. 1992). Reported diseases include canine distemper (Harris 1968, Park 1971), rabies (Serfass et al. 1995), respiratory disease, and urinary infection (Hoover et al. 1984, Route and Peterson 1991). Other reported conditions include jaundice, hepatitis, feline panleucopemia, and pneumonia (Harris 1968). In general, parasites and diseases have not been identified as important factors in river otter population dynamics in the United States, but disease transmittal to otters and other animals by translocating otters is a concern.

Symbiotic and mutualistic interactions

Where river otters and beavers occur together, a facultative commensal relationship exists (Tumlison et al. 1982, Reid 1984, Polechla 1987, 1989) because river otters make extensive use of beaver-created habitat features. River otters benefit from the increased availability of food resources in beaver ponds (Reid et al. 1994a, Dubuc et al. 1990) and commonly use beaver dams, lodges, and bank dens for rest and den sites.

Otters often inhabit beaver bank dens and lodges, sometimes simultaneously with beavers (Melquist and Hornocker 1983, Malville 1990). The regulated flows provided by beaver impoundments also provide stable water supplies, abundant herbaceous cover, and areas of limited human disturbance (Dubuc et al. 1990). Beaver activity over time, particularly in smaller drainages, creates extensive riparian and wetland habitats beneficial to otters (see Habitat section). Beavers do not appear to benefit from the interaction and may occasionally suffer from river otters causing rifts in beaver dams, driving beavers from dens, and occasionally preying on beavers (Reid et al. 1994b).

In colder regions of their range, including Region 2, river otters can serve as part of a pathway for nutrient transport from more productive aquatic systems to less productive terrestrial systems (Ben-David et al. 1998). Crait et al. (2002) hypothesize that cutthroat trout (*Oncorhynchus clarki*) in Yellowstone National Park move nutrients from Yellowstone Lake into nitrogen-poor streams during spawning runs, and that terrestrial fish predators including otters extend the pathway to terrestrial plants by eating trout and excreting nutrients on shore.

CONSERVATION OF RIVER OTTERS IN REGION 2

Threats

The unregulated harvest of river otters for pelts was formerly an important threat to the species and, along with habitat destruction, resulted in large declines in river otter abundance and distribution in North America (Melquist et al. 2003). River otters are now protected from harvest in all Region 2 states. Elsewhere where commercial harvest is permitted, harvest is regulated by state and provincial governments and overseen by the USFWS and Canadian Wildlife Service (CWS) under the auspices of CITES (see Management section). While commercial harvest of otters is no longer regarded as a threat in any part of the river otter's range (Melquist et al. 2003), illegal take of otters and incidental take by beaver trappers may continue to threaten local populations. Predation, parasites, and disease (see Community Ecology section) cause mortality of river otters, but they are not known to have serious impacts on populations (Melquist et al. 2003). The most serious broad-scale threats currently facing river otters stem from the destruction and degradation of habitat and direct human-caused mortality (Melquist et al. 2003).

Habitat destruction and degradation

A primary cause of habitat destruction in Region 2 is water development for economic and recreational purposes, which has reduced flow volumes and altered seasonal flooding patterns in most watersheds (Buskirk et al. 2000). Reduced flows from water diversions can decrease channel depth and even completely dewater stream reaches. Alteration of flow volume or timing (natural hydrograph) can result in changes to stream channel morphology and riparian conditions over time by changing the structure and extent of riparian vegetation, increasing water temperatures or turbidity, and affecting riverbed and floodplain morphology (Ffolliott et al. 2004, Stromberg et al. 2004). Of particular concern in Region 2 are heavily depleted or altered streams, such as the Colorado, Dolores, Gunnison, and San Juan rivers and their tributaries in Colorado. Changes in the structure and function of stream systems that alter system dynamics, reduce flow, reduce or simplify riparian vegetation, or reduce otter prey, adversely affect river otters. Water

depletions can magnify the negative effects of natural drought on river otters.

In large reservoirs, fluctuating water levels usually prevent the establishment of riparian vegetation, and shoreline cover for river otters is poor or absent (M. Ben-David, University of Wyoming, personal communication 2003). Thus, poor quality habitat in large reservoirs may hinder river otter dispersal. Cold-water releases from reservoirs on warm rivers may change the fish and invertebrate fauna downstream. For example, crayfish are a staple of river otter diets in the Green River above Flaming Gorge Reservoir, but crayfish are absent in the colder waters below the dam (Boyd and Ben-David 2002). Compared to the upstream reach, the downstream fish fauna contains fewer slower-swimming, shallow water species that river otters prefer and a greater proportion of fast-swimming salmonids.

Destruction and degradation of riparian vegetation is another serious threat to river otter habitat. Continent-wide, declines of river otters have been most pronounced in low-elevation areas subject to intensive agriculture and urban development, where degradation of shoreline structure and riparian communities has been extensive (Buskirk 2000). In the Humboldt River watershed in Nevada, river otters occupy only remnant areas of intact riparian vegetation. Otters avoid reaches where the floodplain is completely cleared for agriculture; such areas have poor bank stability, and beavers are absent (Bradley 1986). Livestock grazing has affected most riparian areas in the arid southwest, resulting in decreased riparian cover and structural diversity, increased bank erosion and stream down-cutting, and lowered water tables (Clary and Kruse 2004).

Timber harvest can reduce riparian cover, increase stream siltation, and reduce woody debris that provides important cover for fiver otters. River otters in coastal Alaska avoided clearcut areas 5 to 23 years old (Larsen 1983).

River otters in Region 2 may be especially vulnerable to habitat fragmentation because they are largely confined to linear habitats. Stretches of stream habitat made unusable or impassable to river otters can limit the size and viability of river otter populations, inhibit dispersal, and isolate small subpopulations that cannot maintain viability in isolation.

Water pollution

River otters are highly vulnerable to pollution because of their position at the top of aquatic food chains. Residues of petroleum products, mercury and other heavy metals, organochlorine compounds, polychlorinated biphenyls, and other toxic compounds have been found in river otter tissues (Kimber and Kollias 2000, Ben-David et al. 2001a, Bowyer et al. 2003, a review by Melquist et al. 2003). Bioaccumulation of polychlorinated biphenyls was considered the likely cause of river otter declines in Oregon (Henny et al. 1981) and New York (Foley et al. 1988). O'Conner and Nielsen (1981) reported that methyl mercury at dietary levels of 2 ppm was lethal to river otters, and they noted that even after pollution abatement, mercury persisting in sediments continues to move through aquatic food chains.

Physiological, behavioral, and ecological effects on river otters from the *Exxon Valdez* oil spill in 1989 in Prince William Sound, Alaska were studied in particular detail (Ben David et al. 2001b, 2001c, Ben-David et al. 2002, Bowyer et al. 2003). The spill caused initial mortality of river otters by oiling, which was difficult to detect because otters seldom died on open shorelines where they could be detected by beach searches. During 1989-1992, surviving river otters in heavily oiled areas had lower body mass, elevated biomarker compounds in their blood and feces, and larger home ranges, and they ate a less diverse diet and selected habitat differently than otters in control populations (Bowyer et al. 2003). During later studies (1996-1999), differences in these factors were no longer detectable between otters from heavily oiled and lightly oiled areas, and the authors concluded that river otter populations had recovered from the oil spill.

Chronic pollution of waterways in Region 2 that could affect river otters is a greater issue in areas downstream of NFS lands where urban or industrial discharges or agricultural runoff contribute pollutants. Water pollution on NFS lands is primarily confined to areas where past or current mining activity contributes sediments, oils and greases, or heavy metals to rivers and streams (Rudd et al. 1986). Principal areas in Region 2 where historic or current mining activity adversely impacts NFS waterways include the mining districts of the San Juans and central mountains in Colorado, and the Black Hills; coal mining areas of the Grand Mesa, Uncompahgre, Gunnison, and Routt national forests in Colorado; and oil and gas fields in the San Juan and Piceance Basins of Colorado, and the Bighorn, Powder, and Green River basins of Wyoming. Mining can affect water quality by increasing sediment loads and turbidity, by leaching of toxic elements from exposed ore and waste rock, by introducing excess materials from blasting and fertilizer, and by introducing

pathogens from septic systems. Acid drainage associated with mines can seriously degrade water quality and is of particular concern in many historic mining districts in Colorado and the Black Hills. Acid drainage increases water acidity and the solubility of heavy metals, which can severely affect fish and invertebrate productivity (Mason 1981) and lead to direct bioaccumulation of heavy metals by otters through the food chain pathway. Alkaline mine drainage, more typical of coal and surface mining in the western United States, can be just as damaging (Hill 1973, cited in Rudd et al. 1986). The potential for petrochemical pollution to affect river otters in Region 2 is greatest where oil pipelines cross rivers and streams, and where well fields, and oil or fuel storage tanks exist near waterways. Major oil and gas fields in Region 2 include the Powder and Green River basins of Wyoming, and the Piceance, San Juan, and Denver basins of Colorado. Oil pipelines cross most major rivers in Region 2.

Human settlement and recreational use

Human population growth in Region 2 fuels expanding development, often concentrated in floodplains or along streams where land is most easily developed and where scenic and fishing amenities are high. Homes, commercial areas, gravel mining, etc. in floodplains and along streams can degrade riparian and aquatic habitat for river otters. Recreational use of rivers and lakes for boating and fishing is also common and increasing. Shoreline facilities to support recreation can degrade shoreline habitat for otters and concentrate human activities. In general, river otters are shy and will avoid humans when possible, but some will habituate where food is abundant and they are not harassed (Melquist and Hornocker 1983). However, dispersed recreation along waterways at sufficient density may adversely affect river otters by altering habitat use or daily activity patterns (Giere and Eastman 2000).

Human presence in riparian areas introduces domestic dogs, which sometimes kill river otters. Melquist and Hornocker (1983) reported river otters in their Idaho study area killed by dogs, and two river otters reintroduced into Rocky Mountain National Park were killed by canids, presumably domestic dogs associated with human settlement nearby (Colorado Division of Wildlife 2003b).

Increased human presence also increases the risk of mortality from roadkill. In Nebraska, roadkill has been the second most common cause of mortality of reintroduced river otters (Nebraska Game and Parks Commission 2003). In Idaho, roadkill accounted for two

of seven identified mortalities (Melquist and Hornocker 1983), and in Colorado, at least two river otters in the upper Colorado River have been killed on highways (Colorado Division of Wildlife 2003b). Roadkill is an important mortality factor for Eurasian otters in Great Britain (Chanin and Jefferies 1978, Kruuk 1995). Roads with high traffic volume along mountain streams and those providing access to residential and recreational areas along streams and lakeshores are most likely to pose a threat to river otters.

Increased human presence can also result in an increase in the numbers of generalist predators such as coyote, red fox, mountain lion, and raccoon (Goodrich and Buskirk 1995, Buskirk et al. 2000). These species have broad habitat tolerances, switch prey easily, and tend to tolerate or benefit from human development. Generalist predators may affect river otters by increasing predation on young or dispersing otters, or reducing numbers of beavers, which in turn may affect the quality of river otter habitat. Raccoons may compete with river otters for aquatic food.

Introductions of non-native salmonids and other cold-water sport fish into lakes and rivers can reduce prey availability for river otters. In Yellowstone Lake, Wyoming, an unauthorized introduction of lake trout may be reducing populations of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) and reducing food resources for river otters, which may also be declining in the area (Crait et al. 2002). In Region 2, stocking of non-native salmonids is extensive in all major watersheds, particularly at lower elevation reservoirs and tailwater reaches below reservoirs.

Incidental trapping and illegal take

Commercial trapping for beavers and other furbearers is permitted in all Region 2 states except Colorado, where limited beaver trapping is permitted for damage control purposes. Incidental catch of otters in traps set for other furbearers is commonly reported in all Region 2 states. In Nebraska, accidental trapping is the single largest source of mortality among reintroduced river otters (Nebraska Game and Parks Commission 2003). In Colorado, the majority of known deaths of reintroduced river otters have resulted from accidental take in beaver traps (Colorado Division of Wildlife 2003b). The magnitude of this threat in Region 2 is probably variable, and of greatest concern in small populations. Illegal trapping is occasionally a problem. In Nebraska, NGPC law enforcement personnel have investigated a few cases of illegal trapping in recent years. At least one small population of otters was

completely trapped out, presumably for illegal sale out of state (R. Bischof personal communication 2003). Illegal shooting of river otters occurs, but the level of this threat is difficult to assess because most shootings are presumably unreported. In Idaho, one radio-collared otter was killed by gunshot, one recovered from a gunshot wound, and two trapped otters from other areas had shotgun pellets in them (Melquist and Hornocker 1983).

Conservation Status of River Otter in Region 2

Distribution and abundance

The conservation status of river otters in Region 2 has improved markedly since the 1970's because of water pollution abatement, reintroductions, and increased concern for management of otters by Colorado and Nebraska wildlife agencies and Rocky Mountain National Park. However, many areas of formerly occupied habitat in Region 2 remain unoccupied, and river otter populations are more isolated than in pre-settlement times. River otters occur in at least parts of most major watersheds in the Rocky Mountains of Colorado and Wyoming, with the exception of the White, Rio Grande, and headwaters of the South Platte and Arkansas rivers. Distribution in the Great Plains area of Region 2 remains more fragmented, with otters regularly occupying only the Platte and North Platte rivers in Nebraska. The Black Hills National Forest has the most NFS land on the Great Plains with suitable but unoccupied river otter habitat.

No quantitative estimates of river otter abundance or population trend exist continent-wide or in Region 2. Throughout their range, available trapping harvest records and increasing or stable distribution suggest stable or increasing numbers (Melquist et al. 2003). In Region 2, apparent expansions of river otter populations in the Platte River system of Nebraska and the Colorado River watershed of Colorado may indicate increasing numbers of river otters, but no abundance data are available. In Wyoming, river otter populations are perceived to be stable and presumably more numerous than in any other Region 2 state (B. Oakleaf personal communication 2003). Few otters inhabit western South Dakota and Kansas.

River otter populations in Wyoming, Colorado, and Nebraska appear to be persisting and in some cases increasing. In response, Colorado and Nebraska recently down-listed river otters from state endangered to state threatened status. However, concerns remain about the long-term viability of otter populations in these states in the face of increasing habitat loss and degradation, and human-caused mortality. Isolation and small size of some populations may increase their vulnerability to decline or extirpation due to localized or systemic factors. River otters are high trophic-level carnivores that occur in low densities, and are confined to specialized aquatic habitats. Consequently, they require large reaches of suitable stream habitat and are vulnerable to human-caused changes in habitat structure (Buskirk 2000). Habitat degradation and fragmentation are likely to be the most important factors limiting river otter populations and their recolonization of formerly occupied habitats in Region 2. Expanses of waterless terrain and high mountain ranges tend to isolate streams in Region 2. These habitats have been further fragmented by human impacts to streams, lakes, and floodplain wetlands. Impacts from agriculture, urbanization, recreation, and pollution have reduced habitat suitability for river otters in many places, and have fragmented the remaining suitable habitat. Riparian areas on private lands (particularly in semiarid lower elevations) receive little protection and are often subject to destructive land uses. Degraded habitat may create population sinks for river otters, hinder permanent dispersal and colonization, and reduce an otter population's ability to respond to local habitat change by moving (M. Ben-David personal communication 2003).

Vulnerability to human-caused mortality

Human-caused mortality may also be an important factor in river otter conservation in Region 2. The population matrix models described in the **Appendix** showed that survival of adult females is the most important life-history transition for population viability. Most river otter mortality in North America is associated with human causes (Melquist et al. 2003), and the incidences reported in Region 2 states (see Threats section) suggest that this is also true in Region 2.

Vulnerability to habitat change

Natural variations in environmental conditions that may affect river otters include drought, floods, storms, or temporary shifts in prey availability. Otter populations are typically spread widely over large areas, reducing vulnerability to localized environmental variations. Instead, systemic changes to riverine systems will have broader effects on otter persistence. Drought is a concern because the effects can be severe in magnitude and may affect large areas for several years. The mobility of otters may allow them to shift

activity areas temporarily in response to environmental fluctuations, but this requires adequate dispersal corridors. Because river otter population growth rates are sensitive to relatively small changes in adult survival (stochasticity analysis in **Appendix**), widespread or lingering stochastic events such as prolonged drought have the potential to depress river otter populations.

Management of River Otters in Region 2

Implications and conservation elements

Under existing management, river otters in Region 2 are likely to persist at some level in the Rocky Mountains of Wyoming and Colorado, and the Platte River system of Nebraska. Otters may eventually reoccupy the Black Hills in South Dakota and other areas of the Great Plains in Region 2, if suitable habitat remains. However, the river otter has been termed a keystone species because of its role in nutrient transport between aquatic and terrestrial ecosystems, and a sentinel species because of its sensitivity to environmental contaminants and other disturbances (Bowyer et al. 2003). As such, river otter presence should be considered an important element in aquatic and riparian ecosystem health in Region 2 habitats potentially suitable for river otters. The existing and additional management efforts described below should help to make river otter populations across Region 2 more widespread and secure.

State and federal agency planning and management

The state wildlife departments of Colorado and Nebraska have taken an active role in river otter recovery through the implementation of (so far, successful) reintroduction programs and population monitoring. Colorado has a river otter recovery plan and supports research on improved monitoring techniques. Other Region 2 states do not manage river otters other than enforcing prohibitions on take and collecting incidental sightings. A stronger state agency commitment in South Dakota to river otter recovery would increase the chance of successful re-establishment of river otters in the Black Hills. Continued designation by USFS of the river otter as a sensitive species in Region 2 will help direct USFS management actions to benefit river otters. Opportunities exist at forest and district planning levels to direct management to address habitat needs and concerns as outlined in the next section. Maintaining habitat on long stream reaches and maximizing connectivity between protected reaches requires planning across administrative boundaries. Cooperative multi-jurisdictional planning and funding will be necessary to achieve the watershed and landscape management essential to river otter conservation.

Habitat protection and restoration

Where river otters occur, or the potential exists for their recolonization, suitable otter habitat should be maintained, and potentially suitable, but degraded, habitat should be restored where opportunities may exist. At local scales, this requires maintenance of adequate streamflow (at least 50 cfs) and food resources, good water quality, riparian vegetation providing at least 50 percent cover along banks, other cover in or along streams such as woody debris or boulders, and streamflow regimes that protect natural aquatic and riparian processes, ensuring the continued existence of river otter habitat. Actions that alter instream flows, degrade or destroy riparian habitat, eliminate woody debris in streams, or reduce beaver activity should be modified where possible to alleviate impacts to river otter habitat. Principal actions of concern on USFS lands include livestock grazing in riparian areas, timber harvest and fire management where they may affect riparian vegetation or stream siltation, recreational uses and road management along streams and in riparian areas, and water diversion and development projects. Fisheries projects that increase fish (especially native species) and invertebrate biomass are likely to benefit river otters, but replacement of slower-swimming native fish with non-native salmonids may decrease prey availability for otters. Mining and energy development should be managed to avoid water pollution because of the sensitivity of river otters to pollutants. The effects on river otters of habitat modifications at small scales are difficult to discern. However, the cumulative impacts of several modifications over larger spatial and temporal scales are likely more important than the impact of any single project.

At landscape scales, river otter populations in Region 2 require long stream reaches dominated by suitable habitat, and connections between watersheds and between otter populations within watersheds. Because otters require extensive stream reaches of quality habitat and because they exist at low densities, it is likely imperative that subpopulations be interconnected into a metapopulation structure to achieve and maintain viability. Managing habitat for otters at a landscape scale will require identification of key habitat linkages, protection of those linkages from habitat degradation, and the restoration of degraded or severed habitat linkages where necessary.

Much of the known distribution of river otters in Region 2 lies outside of lands administered by the USFS (**Figure 3**, **Figure 4**, **Figure 5**, **Figure 6**, **Figure 7**). Likewise, most of the habitat degradation and fragmentation of concern for river otters has occurred on non-NFS lands at lower elevations, where the impacts of water diversions and impoundments are greatest, and where agricultural and urban land uses have a greater impact on riparian areas. The largest problems are along the Colorado Front Range and in the Colorado River drainage, where human population size and growth rates are the greatest in Region 2. However, suitable river otter habitat is known or likely to exist in all Region 2 national forests. Otter habitat on NFS lands is often more pristine compared to private lands, and thus it may often be more valuable to river otters. As human settlement spreads on lower elevation private lands, NFS lands may be increasingly important in serving as source populations to replenish sink populations on less protected lands. Furthermore, NFS land is key for the dispersal of river otters between watersheds. USFS actions that influence downstream aquatic or riparian conditions may affect river otter habitat on other jurisdictions.

Management for river otter conservation in Region 2 should consider increasing the distribution of river otters into suitable habitats; this is best accomplished by natural colonization, with reintroductions used as a last resort. Sources, locations, and the magnitude of human-caused mortality, including vehicle collisions, predation by dogs, illegal shooting, and incidental take during beaver trapping, should be evaluated, and methods for controlling important causative factors implemented. Note the results of population matrix analysis, indicating that survival of adult females is the most important life-history transition. This will require further development of cost-effective census techniques, their application across a broad range of areas in Region 2, and studies to determine causes of mortality.

Protection of river otters from human-caused mortality will require continuing the existing state commitments to restrict commercial and other take. Additional efforts are needed to minimize proximity of roads, recreational developments, and human settlement to waterways that provide habitat for otters.

Tools and practices

Inventory and monitoring of populations

State agencies in Colorado and Nebraska (described above) and Rocky Mountain National Park

monitor river otter populations. However, because no reliable census technique exists, neither state determines population sizes or densities. Instead, they use sign surveys to provide data on presence and overall distribution of populations, with qualitative evidence on reproduction. These monitoring programs have sufficiently documented the persistence, reproduction, and expansion of reintroduced populations, and have provided an effective basis for conservation planning.

While a sign survey is a cost-effective means to document otter presence, it is not a reliable indicator of abundance because otter density and the amount of visible sign do not correlate well (review by Melquist et al. 2003). Furthermore, slides and sign heaps may be confused with beaver sign. Otters leave abundant sign, including footprints, slides, rolling places, sign heaps, and scat. Sign is most apparent at landings where otters exit the water and at latrine sites. Otters often roll, rub, and groom on sandy or grassy areas along waterways. At these places, otters sometimes twist or scrape vegetation and dirt into mounds and mark the heaps with scent from anal glands. Otters frequently defecate on logs projecting from water, logjams, sandbars, rocks, or similar objects in the water. Winter sign surveys are employed to take advantage of snow for discerning tracks. However, in the Dolores River in southwestern Colorado, where beaver bank dens below ice are plentiful, otters often remain below the ice for weeks, leaving little sign (Colorado Division of Wildlife 2003b). Because otters move over large areas, but may concentrate in areas where food is temporarily abundant, sign surveys should cover as much of the survey area as possible (Melquist and Hornocker 1979).

The Colorado monitoring protocol (Colorado Division of Wildlife 2003b) provides an example for systematic surveys of Region 2 streams accessible by foot or boat. The method specifies:

❖ Use trained observers

❖ Survey entire reach of suspected occupancy

❖ Survey the reach by moving from one end to the other

❖ Complete survey on consecutive days

❖ Survey in early spring prior to high water, or in late summer on some larger rivers where extensive sandbars are exposed

❖ Record otter sightings and sign by location (river km), photograph, written description, and collect scat sample for constituent analysis

❖ Survey each study reach every 5 years.

Based on an average density of one otter per 3.9 km of waterway in Idaho (Melquist and Hornocker 1983), river reaches that contain at least one observed sign for every 5-km section are presumed occupied. Because surveys could record sign from transient otters, population viability must be inferred cautiously from the size of occupied reaches, evidence of reproduction, and population history. Increasing the frequency of surveys would decrease the potential error introduced by transients.

Bridge-sign surveys are especially well suited to areas where otters occur mainly on private lands and where an extensive road network overlaps otter habitats. In Nebraska, bridge-sign surveys are conducted in midwinter to capitalize on snow for maximum track detectability. However, variable snow conditions between years cause bias, so the technique's utility is maximized in areas where winter snow cover is most dependable.

State agencies usually record river otter sightings by trappers and the public to aid in determining the species' distribution (Raesly 2001). In many states, such records constitute the only monitoring effort; within Region 2, these include Wyoming (B, Oakleaf personal communication 2003), South Dakota (A. Kiesow personal communication 2003), and Kansas (M. Peak personal communication 2003). While such observations may provide the only available information in the absence of a systematic monitoring program, Beck (1993) cautioned that public sightings in Colorado have often proved unreliable for determining otter distribution. Misidentification of animals is the biggest problem, but deliberate misreporting may also occur.

Radio telemetry techniques for river otters have mostly focused on subcutaneous and interperitoneal implants, because the otter's tapered neck makes collars unworkable. Radio implants require an operation by a veterinarian and are costly and intrusive to animals. Sauer et al. (1999) developed an adaptive kernel technique for estimating river otter home ranges, and Blundell et al. (2001) made additional refinements.

Because river otters are sparsely distributed, populations cover large areas, and monitoring of population size in the strict sense requires a regional scale. Otter population boundaries in Region 2 are conveniently defined by a single watershed, and some populations may be further separated within a watershed by areas of unsuitable habitat. Because the headwaters of many streams, often of multiple watersheds, frequently originate on national forests, forests or even districts may contain parts of several otter populations that extend beyond NFS lands. Population monitoring would be most meaningful when done on a watershed scale, encompassing multiple land jurisdictions.

Until recently, precise determination of river otter abundance has required marking and studying individual otters by radio telemetry, in conjunction with other evidence drawn from various field techniques (Melquist and Hornocker 1979, 1983, Melquist and Dronkert 1987). However, recent advances in molecular genetic techniques now allow researchers to gather a variety of information from otter fecal and hair samples for species and even individual identification (Melquist et al. 2003). DNA extracted from intestinal cells shed with feces can be analyzed to generate genetic profiles and to identify individual animals. Systematic fecal collection followed by genetic typing and analysis of sex-specific probes can provide rapid estimation of population size and sex ratios while avoiding the expense and intrusiveness of capture and handling animals (Melquist et al. 2003, Hansen 2004). Research underway in Colorado is investigating the use of non-lethal snares to collect hair from river otters, then using DNA fingerprinting to identify individuals and to estimate population size (P. Schnurr personal communication 2005). Genetic techniques have also been employed to investigate other aspects of river otter ecology. Blundell et al. (2002b) used microsatellite markers and radio telemetry to assess sex-biased dispersal in coastal Alaskan river otters, and to estimate the potential for recolonization following local extirpation. Following the Exxon Valdez oil spill in Alaska, Bowyer et al. (2003) demonstrated the use of fecal porphyrins and other substances as biomarkers to detect different levels of contaminants and contribute to a health assessment of otter populations.

River otters can be live-captured using Hancock traps (Northcott and Slade 1976, Melquist and Hornocker 1979) or soft-catch leg-hold traps (Serfass et al. 1996). Blundell et al. (1999) evaluated efficacy and injury concerns of the two methods. Captive otters can

be immobilized with a variety of drugs (Hoover 1984, Hoover et al. 1985a, Hoover and Jones 1986, Spelman et al. 1993), preferably Telazol (M. Ben-David personal communication 2005).

CNHP (2002) reviewed otter population monitoring techniques, including abundance estimates derived from track counts in snow (Reid et al. 1987, St-Georges et al. 1995), mark-"recapture" with radioactive isotopes injected into animals and recovered in feces (Knaus et al. 1983, Testa et al. 1994), catch per unit effort (Chilelli et al. 1996), latrine surveys (Mason and Macdonald 1986, Swimley and Hardisky 2000), and scent-station surveys (Humphrey and Zinn 1982, Eccles 1989). Of these, latrine surveys and scent-station surveys have been the most often applied in the United States to estimate otter abundance. Latrine surveys are currently used to estimate otter abundance and distribution in Rocky Mountain National Park (Herreman and Ben-David 2002) and throughout Pennsylvania (Swimley and Hardisky 2000). However, the technique has been questioned for North American river otters (Melquist and Horncocker 1983) and Eurasian otters (Kruuk and Conroy 1987, Hutchings and White 2000) because the abundance of otter scats and other sign does not correlate well with otter abundance. Annual latrine surveys in spring and fall in Rocky Mountain National Park have shown seasonal variation; for the years 2001 through 2005, latrine site density in fall was 8 to 58 percent of the density for the same study reach the previous spring (Herreman and Ben-David 2002; unpublished Investigator's Annual Reports, Rocky Mountain National Park). The number of scats per latrine site was also less in fall. To provide an effective index to otter abundance, sign surveys at a given study reach should be conducted during the same season each year.

Nebraska is the only state in Region 2 that attempts to monitor otter abundance statewide. NGPC uses bridge crossing sign survey data to estimate otter density. Abundance is derived by extrapolating from the number of sign observations using assumptions about otter home range size (R. Bischof personal communication 2003). Population trend is inferred by comparing annual estimates of abundance and distribution, as well as ancillary sightings and incidental trap records provided by the public. Abundance and trend estimates are considered coarse and must be interpreted with caution. Oklahoma uses a similar monitoring system (Shackelford and Whitaker 1997).

Inventory and monitoring of habitat

Many states have developed habitat inventory and evaluation procedures to guide and prioritize river otter reintroductions (Raesly 2001). A habitat evaluation form and methodology for Colorado (Dronkert 1983) provides a good framework for rating and comparing otter habitats. The method requires evaluation of the following:

❖ Potential for site protection and cooperation by landowner

❖ Stream length

❖ Water quality

❖ Amount of open water available in winter

❖ Availability of den sites (including beaver activity) and riparian cover

❖ Availability of fish and crustacean prey

❖ Trapping pressure

❖ Recreational use

❖ Other development pressure (e.g., mining, highways, residential development)

❖ Probability of future conflicts from land use changes.

The form provides scores for levels in each category, and then the scores are summed to rank and compare habitat sites. While the form was designed to evaluate reintroduction sites, it also would be useful to evaluate and monitor habitat for existing populations and to guide habitat restoration efforts. The procedure could be modified to include less subjective categories and to provide for the measurement of habitat variables, to the extent that the value of various characteristics to river otter habitat is known. Additional habitat characteristics recommended for inventories in Region 2 include stream gradient (with stream classes A and B [Rosgen 1994] identified as high value, class C as moderate value, and class D as low value), and stream volume (minimum flow and annual average flow).

No state within Region 2 currently implements a habitat monitoring program for river otters. The above procedures for habitat inventory could be used periodically to monitor habitat quality for river otters.

Population and habitat management approaches

Throughout the United States and Canada, river otter management strategies include furbearer harvest management, reintroductions, population monitoring, and conservation planning. Management approaches vary in Region 2 states, depending on the species' status and remaining habitat potential. In Wyoming, where river otters are widespread and believed to be secure, there is no species management program. Management to protect watersheds and riparian conditions generally benefit river otters. Likewise, in South Dakota and Kansas, where river otters are severely reduced, no active management exists. River otters are beginning to recolonize some areas from adjacent states, but western parts of the states within Region 2 provide little habitat. Reintroductions and active conservation planning and monitoring in Colorado and Nebraska have restored river otter populations to several watersheds, from which otters are gradually recolonizing portions of remaining habitat.

Furbearer harvest management

Where river otter harvest is allowed, monitoring of populations remains a difficult issue. State and provincial agencies typically rely on analysis of sex and age ratios determined from harvest samples to identify current or impending overharvest (Dixon 1981), but other data are required to determine population dynamics (Caughley 1974). Chilelli et al. (1996) reviewed the estimation of river otter population trends from harvest data and proposed improvements, including standardizing age estimation procedures, incorporating catch-per-unit-effort estimates, and analysis at regional scales.

States and provinces that allow commercial harvest of river otters set seasons and/or quotas for geographic areas to control harvest rates. Most states with concerns about reduced otter populations (including all Region 2 states) do not allow commercial harvest, and they prohibit, by statute, the killing or harassment of river otters. Such prohibitions are generally effective in controlling commercial harvest, but they are less effective in controlling illegal shooting, incidental take by beaver trappers, and deaths of river otters by vehicle collisions, dogs, and other human-related causes.

Reintroductions

Reintroductions have helped to restore river otter populations in many states. Prerelease care and clinical evaluation procedures have been thoroughly described (Hoover 1984, Hoover et al. 1984, 1985b, Serfass and Rymon 1985, Serfass et al. 1993, 1996). Reading and Clark (1996) provided a critical review of carnivore reintroductions and a theoretical framework for evaluating and planning reintroductions for maximum success.

River otter restoration has involved extensive reintroductions to replace extirpated populations or to bolster low native populations (Raesly 2001). From 1976 through 1998, 4,018 river otters were reintroduced in 21 states and the province of Alberta. Reintroductions have generally proven successful, with 83 percent of projects reporting evidence of reproduction and 77 percent indicating range expansion of reintroduced populations (Raesly 2001). Within Region 2, reintroductions in Colorado and Nebraska have generally been successful in establishing reproducing and expanding populations. However, it is important to note that reintroductions are costly, exert considerable risk of stress and mortality on translocated animals, and may have unintended effects on the genetic composition of existing populations. For these reasons, reintroductions should be considered as the last resort for reestablishing river otter populations.

Conservation planning

The Draft State of Colorado River Otter Recovery Plan (Colorado Division of Wildlife 2003b) provides a framework for managing the recovery of river otters in the region. The plan calls for the re-establishment of at least three river otter populations in the state, with each population continuously occupying at least 120 km of river. The plan also calls for maximizing connectivity between populations, and it describes procedures for monitoring occupancy by systematic sign surveys every 5 years. More frequent sign surveys would increase the effectiveness of detecting gross population trends or changes in abundance (M. Ben-David personal communication 2005), but funding is inadequate. Of greater concern, is the apparent inadequate reach of the plan's goals and objectives in defining recovery. Achieving the plan's objectives could result in as few as three populations of only about 30 otters each. Populations of this size are likely far too small to be independently viable in the long term without ongoing management intervention, such as continued translocations (M. Ben-David personal communication 2005). Planning for the recovery of self-sustaining river populations will require the establishment of a network of populations connected into an effective metapopulation structure over large areas.

The Nebraska Game and Parks Commission conducts annual monitoring of river otters by sign surveys at bridge crossings (Bischof 2002), but does not have a long-range plan for river otter conservation. Kiesow (2003) evaluated potential river otter reintroduction sites in South Dakota based on river habitat, water quality, and prey availability, and concluded that the most feasible reintroduction sites were the Bad, Big Sioux, James, North Fork of the Whetstone, and Little White rivers. While Kiesow (2003) developed a river otter reintroduction protocol for South Dakota, the state is not planning to address river otter recovery.

Suggested future direction for management

Multi-agency and multi-state planning at regional and watershed scales should be undertaken to establish and maintain large interconnected habitat blocks capable of sustaining metapopulation structure. Suitable habitat could be mapped using a geographic information system (GIS) and this could be used to analyze river otter distribution, metapopulation characteristics, habitat connectivity, and likely dispersal routes. Suggested parameters for modeling otter habitat in Region 2 include, as a minimum, streams with a permanent flow of at least 10 cfs and at least 50 percent vegetation cover along banks (M. Ben-David personal communication 2005).

Management direction within identified habitat blocks would include:

❖ maintain adequate instream flow, water quality, and riparian habitat conditions to sustain river otters and their prey

❖ re-establish river otter populations where appropriate to expand or establish functioning metapopulations and to increase subpopulation connectivity

❖ monitor habitat conditions and river otter presence over broad scales and at time intervals sufficient to detect major population contractions as early as possible

❖ collect anecdotal evidence of reproduction during sign surveys to help interpret presence-absence data.

Where populations are declining in range or not sufficiently expanding, managers should attempt to identify the responsible factors (e.g., excessive mortality or deteriorating habitat conditions) and to address them with improved management. Human-caused mortality of river otters can and should be controlled to the degree possible. Incidental catch of river otters can be reduced by proper trap method and placement. Where river otters occur, use of foothold traps and snares instead of conibear traps is recommended so that captured otters can be released. Snares with large loops (9 to 10 inches) help reduce otter capture. If conibear traps are used, triggers should be placed straight down near the sides of the trap to reduce the chance of river otter capture. Traps should not be placed in likely river otter travel routes, such as trails crossing beaver dams and entrances to beaver bank dens and lodges (A. Kiesow personal communication). The International Association of Fish and Wildlife Agencies (2003) Furbearer Resources Technical Work Group is developing Best Management Practices (BMPs) to guide furbearer trapping in each of five regions in the United States. BMPs will recommend traps and set procedures to maximize efficiency, selectivity, and animal welfare. Other sources of human-caused mortality must be controlled through local and regional planning that addresses human intrusion of roads, recreational trails, and developments into important river otter habitats.

Information Needs

Melquist et al. (2003) provided a thorough review of river otter research and management needs. Although much research has been conducted on river otter/habitat relationships since the late 1970's, the need continues for research and population monitoring. CITES requires states and provinces that allow commercial harvest of river otter to monitor populations or to restrict trade. Region 2 states, which do not currently allow commercial harvest, have obligations to conserve river otters as state threatened species (Colorado, South Dakota, and Nebraska) or protected species (Wyoming and Kansas). The most reliable population data are still derived from costly radio telemetry studies. Population indices, as described in the Tools and Practices section, are much cheaper and less intrusive, but they generally fail to provide accurate and reliable population trend data on a regional scale. Among the most important informational needs for river otter conservation in Region 2 is development of reliable and cost-effective techniques for annually monitoring population size and trend.

Other information needs identified by Melquist et al. (2003) include:

- ❖ explore the use of otter population monitoring as a "flagship species" to monitor wetland conditions, water quality, contaminants, and levels of human disturbance

- ❖ improve river otter population models; in particular, re-evaluate the potential reproductive contribution of female sub-adults

- ❖ examine the importance and use of otter latrine sites as this information will improve interpretation of latrine site surveys for population monitoring.

The distribution of river otters is reasonably well known throughout much of Region 2. The greatest attention by agency biologists has been in Colorado and Nebraska, particularly in areas where reintroductions have occurred. Rocky Mountain National Park continues to monitor the status of river otters annually in the park and adjacent areas, and current research on otters on the Green River and Yellowstone National Park in Wyoming contributes to our understanding of distribution in those areas.

The response of river otter populations to changes in habitat is poorly understood and represents a challenge to management planning. Of particular concern in Region 2 is drought, which tends to affect lower elevation stream reaches the most. While reasonable assumptions can be made about the effects of wholesale destruction of habitat, the direction and magnitude of population responses to less drastic habitat conditions are more difficult to predict. For example, dewatering of rivers can be expected to eliminate otter use, but the effects of flow reductions or alterations in seasonal flow patterns are unknown. Such effects are likely to be complex because they may involve aquatic habitat, terrestrial habitat, prey availability, or relationships among all three. The commensal relationship between river otters and beavers must also be considered. Habitat changes that affect beaver abundance or habitat use are also likely to affect river otters by changing den site availability, prey availability, and the long-term influence of beaver activity on the structure and function of riparian and aquatic systems.

The influence of incremental human development on otters is also poorly understood. Greater knowledge of thresholds of human occupancy in river otter habitats would increase understanding of potential effects through disturbance, roadkills, and dogs.

Another information need is seasonal movement patterns. Intensive studies using radio telemetry have shown that some otters make significant seasonal movements to exploit ephemeral food sources. This may not occur in all populations to any extent, but it is impossible to determine without detailed study. As a result, predicting the impacts of short-lived disturbances in a part of occupied habitat, or disturbances that create temporary obstacles to river otter movement is made more difficult.

The ability of river otter populations to expand and naturally recolonize areas from which they have been extirpated is not well understood. Evidence exists from Great Plains states and Colorado of reintroduced river otters dispersing long distances into connected river systems, but the extent to which dispersing otters can re-establish viable populations is mostly unknown. A spatial model of river otter dispersal capability developed for coastal river otters in Alaska is currently being applied to river otter populations in the upper Colorado River Basin to assess the likelihood of natural recolonization of river otters into the Grand Canyon from existing populations in the upper Colorado and Green rivers (Boyd and Ben-David 2002). This type of model could be applied throughout Region 2 to estimate natural colonization rates, to identify barriers to otter dispersal, and to plan for the regional conservation of otters.

Fish populations in much of Region 2 are fairly well monitored because of the importance of sport fisheries, the presence of federally-listed fish species in some areas, and the interest in water quality and river management. As a result, fish population responses to the most common perturbations, especially changes in flow, temperature, turbidity, and sedimentation, are reasonably predictable, at least for sport fish and more common non-game species. Crayfish have received comparatively little study, and this represents a significant knowledge gap for management of river otter populations where crayfish are an important diet constituent.

Demographic issues for small river otter populations are insufficiently understood to be certain that populations will persist. Many of the reintroduced populations in Region 2 outside of Wyoming are small, and pathways and magnitude of gene flow are not yet apparent. The Piedra River population in the San Juan

National Forest is probably the most isolated population in the Region, and one of the smallest. Founder effects and other problems of small populations may become important. Other populations in the Region have at least potential pathways of dispersal and gene flow that could link them to other populations, but rates of gene flow between watersheds and to what extent those rates differ from pre-disturbance conditions are unknown.

The greatest and most immediate information need is a cost-effective technique to monitor population trend. Radio telemetry in association with detailed field studies has been the only method that provides unequivocal counts that can be compared over time to assess trend. The use of DNA fingerprinting from fecal material (Hansen 2004) or hair (dePuis 20006) to identify individuals provides the most promise for a new cost-effective technique for abundance estimation.

Research priorities for conserving river otters in Region 2 involve increasing the understanding of how and why population numbers and distribution change. The fundamental questions that cannot currently be answered include:

❖ how many river otters now exist in each population?

❖ is each population increasing, stable, or decreasing?

❖ what effects will current and anticipated human activities have on otter population trends?

❖ to what extent are populations linked to each other?

❖ what could happen to populations that remain small and isolated, despite the best land management decisions?

Answering these questions will require:

❖ development of cost-effective and widely applicable census methods

❖ increased understanding of the effects of river flow perturbations, dams and reservoirs, water pollution, sedimentation, riparian habitat destruction, and increasing human settlement and recreation on otters and their ability to move freely through waterways

❖ an understanding of thresholds of acceptable habitat alterations, and the ways in which different stresses interact to create cumulative effects

❖ knowledge of the genetic structure of populations, pathways and rates of gene flow, dispersal rates and abilities, minimum viable population sizes, and the relative risk of extirpation associated with populations that are below the minimum threshold.

Some data may exist that could not be incorporated into this report. For example, anecdotal observations of river otters by USFS and other agency or private sector biologists could extend the known range of river otters and confirm expansion of otters into some historical ranges where they are not shown in the range maps. Anecdotal observations from knowledgeable members of the public, including trappers, fishermen, and naturalists can also be useful to direct further investigations.

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APPENDIX

Matrix Population Model for the River Otter

Life cycle graph and model development

Matrix demographic models facilitate assessment of critical transitions in the life history. A key first step is to create a *life cycle graph*, from which to compute a *projection matrix* amenable to quantitative analysis using computer programs (Caswell 2001). We formulated a life cycle graph for river otter (**Figure 8** in the assessment) that comprised four stages, and a matrix population model with a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001). Model inputs (vital rates such as survival and fertility) are shown in **Table A1**. Stage 1 represents females in their first year, with "breeding" (i.e., giving birth) probability equal to 0 (Melquist et al. 2003). Stage 2 represents second year females, with breeding probability equal to 0.05. Births by second-year females have occasionally been reported, but most females do not reach sexual maturity until their second year, giving birth in their third year because of delayed implantation (studies reviewed by Melquist et al. 2003, Toweill and Tabor 1982). Stage 3 represents females that bred in the previous year. Stage 4 represents females in at least their third year that did not breed the previous year. After first breeding, females generally alternate between Stage 3 and Stage 4. Stages 3 and 4 in the life cycle graph address the fact that the birth interval for otter females varies from one to two years (reviews by Melquist et al. 2003, Melquist and Dronkert 1987, Toweill and Tabor 1982). No data on birth intervals are available from otters in Region 2 states. High pregnancy rates of adult females reported for otter populations subject to trapping harvest in Oregon (99%; Tabor and Wight 1977) and Missouri (about 90%; Missouri Department of Conservation, unpublished data) indicate that most females in those populations bred every year. Other

studies in the northeastern and southern U.S. reported near 0 to 25% of females giving birth in consecutive years (Toweill and Tabor 1982). We selected a conservative probability for breeding in consecutive years of 0.25.

Survival rates for the model (**Table A1**) were 0.53 through the first year and 0.79 thereafter. These values were determined by averaging age-class population structure data presented by Toweill and Tabor (1982) for river otter populations in Oregon, Maryland, and Alabama-Georgia, then slightly modifying the adult survivorship value to correspond to an assumed population growth rate ($\lambda = 1.008$) close to 1.0 (that is, essentially stationary). Our adult survivorship value is similar to values reported for river otters in coastal Alaska (about 90%; Bowyer et al. 2003), wild-caught river otters reintroduced in North America (46-91%, cited in Bowyer et al. 2003), and Eurasian otters in Shetland (about 85%; Kruuk and Conroy 1991) and Sweden (79%; Sjoeasen 1996).

Sensitivity analysis

Sensitivity is the effect on λ of an absolute change in the vital rates a_{ij}, the arcs in the life cycle graph (**Figure 8** in the assessment) and the cells in the matrix, **A** (**Table A2** and **Table A3**). Sensitivity analysis provides several kinds of useful information (Caswell 2001). First, sensitivities show how important a given vital rate is to λ and, by inference, fitness. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from inappropriate or biased estimation techniques or other errors of analysis. To improve the accuracy of population models biologists should concentrate on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever these can be linked to effects on stage-specific survival or fertility rates. Fourth,

Table A1. Parameter values for the component terms (P_i, B_i, and m_i) that make up the vital rates in the projection matrix model for river otter.

Parameter	Numeric Value	Description
m	1.17	Number of female offspring produced by a female
P_1	0.53	Survival through first year
P_a	0.79	Survival through years after the first year
B_2	0.05	Probability of breeding in second year of life
B_3	0.25	Probability of breeding in any two successive years

Table A2. Symbolic values for the cells in the projection matrix, **A** (with cells a_{ij}) corresponding to the life cycle graph shown in **Figure 8** of the assessment. Each cell represents a vital rate such as survival or fertility and corresponds to an arc in the life cycle graph. The top row represents fertility transitions, with compound terms describing probability of breeding (B_i), survival of the mother (P_i) and offspring production (m_i).

Stage	1	2	3	4
1		$P_a B_2 m$	$P_a B_3 m$	$P_a m$
2	P_1			
3		$P_a B_2$	$P_a B_2$	$P_a(1\text{-}B_3)$
4		$P_a(1\text{-}B_2)$	$P_a(1\text{-}B_3)$	$P_a B_3$

Table A3. Numeric values for the cells in the projection matrix, A, corresponding to the life cycle graph shown in **Figure 8** of the assessment.

Stage	1	2	3	4
1	0	0.046	0.231	0.924
2	0.439	0	0	0
3	0	0.040	0.198	0.593
4	0	0.751	0.593	0.198

managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing λ.

Table A4 shows the "possible sensitivities only" matrix for this analysis. In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. For example, any factor that changes the annual survival rate of Stage 3 females is likely to cause similar changes in the survival rates of other adult female age classes. Therefore it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the greatest sensitivity of λ was to changes in "adult" survival (1.71; 71.2% of total). First-year survival sensitivity was 0.37 (15.3% of total) and the summed "fertility" sensitivity was 0.32 (13.4% of total). The river otter shows most of the sensitivity of λ to changes in survival (86.5%). The major conclusion from the sensitivity analysis is that survival, especially of adult females, is the key to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For example, a change of 0.5 in survival may be highly significant to population viability (e.g., a change from 90% to 40%). However, a change of 0.5 in fertility may be a very small proportional change (e.g., a change in litter size from 3.5 to 4.0). Elasticities are the sensitivities of λ to *proportional* changes in the vital rates (a_{ij}) and thus partially avoid the problem of differences in units of measurement. The elasticities also have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute

Table A4. Sensitivity matrix, **S** (with cells s_{ij}) for the river otter. The three transitions to which λ of river otter is most sensitive are in bold. Only those sensitivities for which a_{ij} is non-zero ("possible sensitivities") are shown.

Stage	1	2	3	4
1		0.07	0.109	0.144
2	**0.368**			
3		0.168	0.261	**0.346**
4		0.751	0.593	**0.418**

(guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of fertility (F_i) and survival (P_i) for a given species.

Elasticities for river otter are shown in **Table A5**. λ is most elastic to changes in P_a, the survival of "adult" individuals (those in Stages 2 to 4; summed elasticities = 67.9%), followed by equivalent values (16% each) for first-year survival, P_1, and the summed fertility (the F_i transitions) of all 3 reproductive stages. The relative magnitudes of sensitivities correspond fairly closely to those of the elasticities. Thus, both analyses suggest that survival rates of adults are the population characteristics most important to population viability.

Other demographic parameters

The Stable (St)age Distribution (SSD, **Table A6**) describes the proportion of each stage (or age-class) in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable stage distribution, regardless of whether the population is declining, stationary, or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For river otters at the time of the post-breeding annual census (just after the end of the breeding season), first-year individuals represent 33.2% of the population, and second-year individuals represent 14.5% of the population. The third stage ("adults" in their "off" year for breeding) represents 22.5% of the population, while individuals in Stage 4 ("adults" in their "on" year) represent 29.8% of the population. Because the matrix contains information on time required for transitions, one can calculate the mean and variance of ages for stages that are heterogeneous for age (Cochran and Ellner 1992), as shown in **Table A6**.

Reproductive values (**Table A7**) describe the "value" of a stage as a seed for population growth relative to that of the first stage (Caswell 2001). The reproductive value of the first stage is always 1.0. A female individual in Stage 2 is "worth" 2.3 first-year

Table A5. Elasticity matrix, **E** (with cells e_{ij}) for the river otter. The three transitions to which λ of river otter is most elastic are in bold. Note that the elasticities sum to 1.

Stage	1	2	3	4
1		0.003	0.025	0.132
2	**0.16**			
3		0.007	0.051	**0.204**
4		0.151	**0.185**	0.082

Table A6. Stable stage distribution (SSD), indicating the proportion of the population in each of the stages at the time of the census, and means and variances of ages of the stages for the river otter model.

Stage	Description	SSD	Mean age (± SD)
1	First-year females	0.332	0 ± 0
2	Second-year females	0.145	1 ± 0
3	"Off-year" adults	0.225	6.3 ± 4.1
4	"On-year" breeders	0.298	5.1 ± 4.0

Table A7. Reproductive values for female river otters. Reproductive values can be thought of as describing the "value" of an age-class as a seed for population growth, relative to that of the first (newborn) age-class, which is always defined to have the value 1.0.

Stage	Description	Reproductive Values
1	First-year females	
2	Second-year females	
3	"Off-year" adults	
4	"On-year" breeders	

females, and so on. The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage, discounted by the probability of surviving (Williams 1966). The peak reproductive value (2.9) is for Stage 4 "adult" females in their "on" year. The reproductive value results corroborate those of the sensitivity and elasticity analyses. Survival of older reproductive females that are the mainstay of the population is critical to the population dynamics of river otters. The cohort generation time for river otters is 6.4 years (SD = 4.2 years). Cohort generation time is the population turnover time important to the rate of evolutionary change.

Stochastic model

We created stochastic matrix models for river otters. The goals of these models were 1) to assess the relative importance of different degrees of stochasticity (how does the amount of variability in the environment affect population dynamics?), and 2) to assess whether variability would have dramatically different effects depending on the transitions varying (e.g., does variable early survival have a greater impact than variability in fertility?). We incorporated stochasticity in several ways, by varying different combinations of vital rates and by varying the amplitude of stochastic fluctuation (**Table A8**). Under Variant 1 we altered the "adult" survival rates (P_a). Under Variant 2 we varied only first-year survival, P_1. Under Variant 3 we varied m, the number of offspring per female. Each run consisted of 2,000 census intervals (years) beginning

with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) under the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. Each simulation consisted of running 100 replicate populations (each for 2,000 yearly census intervals). We varied the amplitude of fluctuation by changing the standard deviation of the beta distribution from which the stochastic vital rates were selected. The beta distribution has the desirable property that it is bounded on the interval 0-1, preventing selection of biologically impossible vital rates (e.g., survival greater than 1.0). The default amplitude was a standard deviation of one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Variant 4 affected the same "adult" survival rates as Variant 1, but was subjected to only half the variability (SD was 1/8 rather than 1/4 of the mean). We calculated the stochastic growth rate, $log\lambda_s$, according to Equation 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model produced two major conclusions. The first major conclusion is that altering the "adult" survival rates had a much more dramatic effect on λ than altering either all the fertilities or the first-year survival. For example, under the most variable adult survival rates (P_a) of Variant 1 (SD =1/4 of mean) all 100 replicate populations went extinct, with a mean time to extinction of 231 census intervals. In contrast, Variants 2 and 3, affecting first-year survival and

Table A8. Results of four variants of stochastic projections for river otters. Stochastic fluctuations have the greatest effect when acting on "adult" survival rates (Variant 1).

	Variant 1	Variant 2	Variant 3	Variant 4
Input factors:				
Affected cells	P_a	P_1	m	P_a
S.D. for beta distribution draw	1/4	1/4	1/4	1/8
Output values:				
Deterministic λ	1.008	1.008	1.008	1.008
# Extinctions/100 trials	**100**	0	0	**24**
Mean extinction time	231	N/A	N/A	1,282
# Declines/# surviving populations	—	0/100	0	46/76
Mean ending population size	—	5,832,941	6,086,876	285,892
S.D.	—	1,620,483	1,393,600	822,062
Median ending size	—	5,611,363	5,706,813	5,362
Log λ_s	-0.0424	0.0032	0.0032	-0.0017
λ_s	0.959	1.0032	1.0032	0.9983
Percent reduction in λ	4.92	0.49	0.48	0.96

fertility respectively, had all 100 replicates growing to population sizes much larger than the starting size. Even after reducing the amplitude of the stochastic variation in "adult" survival under Variant 4, long-term λ_s was still lower than that for the Variants 2 and 3. Under Variant 4, 24 of 100 replicates went extinct, and a further 46 declined from the starting population size.

Variants 1 and 4, varying adult survival, were the only stochastic models that resulted in a change from $\lambda > 1$ to $\lambda < 1$, and the only models that resulted in extinctions. This difference in the effects of stochastic variation was predictable from the sensitivities and elasticities (**Table A4** and **Table A5**). λ was much more sensitive and elastic to variability in "adult" survival than it was to variability in the entire set of fertilities, F_i or to changes in first-year survival.

The second major conclusion is that higher-amplitude stochasticity has a detrimental effect on population dynamics. This detrimental effect occurs despite the fact that the average vital rates remain the same as under the deterministic model. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001, pp. 390-392).

The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Given sufficient variability in a vital rate to which λ is elastic, any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. These results suggest that populations of river otters are relatively tolerant to stochastic fluctuations in fertilities and first-year survival rates, but highly vulnerable to high variability in the survival of adult stages. Pfister (1998) showed that for a wide range of empirical life histories, high

sensitivity or elasticity is negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that human-caused impacts may induce variation in previously invariant vital rates (such as annual adult survival), with consequent negative effects on population dynamics.

Refining the models

Improving the data on survival rates would greatly increase the accuracy of these analyses. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variation ins vital rates. Using observed correlations would improve on this assumption by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits.

Other potential refinements include incorporating density-dependent effects. At present, data are insufficient to assess reasonable functions governing density dependence. The present model also incorporates a fairly simple alternation of breeding (100% probability) with low probability of breeding in the following year (25%). Improved data on probability of breeding in successive years would allow more sophisticated analysis of fertility. The extent to which environmental conditions influence fertility is of paramount concern in this regard.